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Cover photo: Female wolf spider, *Rabidosa rabida* (Araneae, Lycosidae) with hatchlings that recently emerged from the egg sac still attached to her spinnerets. (*Photo by Robert Suter*)

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REVISION OF THE SPIDER GENUS *NEOANAGRAPHIS* (ARANEAE, LIOCRANIDAE)

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ABSTRACT. The spider genus *Neoanagraphis* consists of two partially sympatric species, *N. chamberlini* Gertsch & Mulaik 1936 and *N. pearcei* Gertsch 1941. Herein I review the genus which is now transferred from the Clubionidae to the Liocranidae, provide a distribution map and describe the females for the first time. Over 55% of the specimens of both species examined in this study came from the Nevada Test Site (i.e., atomic bombing range) in southern Nevada. Collection phenology at this site showed almost non-overlapping temporal activity for the males and habitats for each species within this area. Immatures from the Nevada Test Site also could be separated where the ventral anterior tibia spination and habitat dichotomy matched that of the adults. If this extrapolation holds throughout the distribution and there are no additional species, one should be able to accurately identify immatures of any size to species.

Keywords: Arachnida, taxonomy

The spider genus *Neoanagraphis* was erected in 1936 with the naming of the type species, *N. chamberlini,* based upon one mature male which was initially assigned to the family Gnaphosidae (Gertsch & Mulaik 1936). A second species, *N. pearcei,* was later described, again from a single male specimen and the genus was transferred to the family Clubionidae (Gertsch 1941). From this point, *Neoanagraphis* is scarcely mentioned in the literature except in faunal surveys (Allred et al. 1963a; Allred & Gertsch 1976; Allred & Kaston 1983; Jung & Roth 1974; Ryckman & Lee 1956).

Neoanagraphis is a rather non-descript looking "clubionoid" spider with the exception of the unique characteristic that the tarsal claws of legs III and IV are extremely long with few teeth at the base (Fig. 1). Here I review this genus of spiders and describe the females of both species for the first time.

The acronyms used in this paper are as follows: AMNH = American Museum of Natural History, N. Platnick; CAS = California Academy of Science, C. Griswold, D. Ubick; CDFA = California Department Food & Agriculture, Visalia, California, M. Moody; JLO = J.L. Ortiz, Laguna Niguel, California; NMSU = New Mexico State University Arthropod Museum, D. Richman; UCR = Entomology Museum, University California-Riverside; VDR = V.D. Roth, Portal, Arizona; WRI = W.R. Icenogle, Winchester, California.

METHODS

All specimens were examined under alcohol with a Wild M5 Microscope with ocular micrometer. Leg measurements and spination pattern were taken from 20 spiders of each gender of each species where possible; spiders used here had at least four legs from the same side of the body intact. (Many specimens were collected in pitfall traps and, hence, were desiccated with multiple disarticulated limbs). Explanation of spination pattern: 1-1-1 represents surface having 1 basal and 1 distal spine with 1 median spine equidistant between them, 1-1-0-2 represents surface with 1 basal and 2 distal spines with 1 median spine about twice as far from distal as the basal. Where possible, up to half of each cohort of 20 originated from the Nevada Test Site (NTS). All mature spiders examined in this study were measured for cephalothorax and abdomen widths and lengths as well as cymbium length or epigynal plate width and length. Epigynal plate width was measured as the distance between the median aspects of the base of the lateral spurs; epigynal plate length was measured from the epigynal plate width line to the posterior tip of the plate. All measurements in the paper are presented in millimeters and the limits of the range are presented in parenthe-

Figure 1.—Leg IV tarsus of *Neoanagrapnis* showing the long, nearly unarmed claw.

ses. Additional methods are described under sections where pertinent. Elevation data not recorded on the specimen label were obtained in correspondence with either the original collector or with arachnologists familiar with the collection locale.

Live-captured mature specimens (2♂, 1♀) were boiled in water for 5 min to splay the spinnerets. They were preserved in 70% alcohol and sent to the AMNH for examination to determine whether the genus would remain in the Clubionidae.

KEY

1. Anterior tibia with two pairs of ventral spines (apicals weak if present); tip of embolus short, blunt, appearing often as folded flap (Figs. 2, 3); posteriorly-directed epigynal plate usually as long as wide or longer, usually V-shaped and usually extending to the posterior edge of the spermathecae or beyond (Fig. 4, 5) . . *chamberlini*
2. Anterior tibia with three pairs of ventral spines (apicals weak if present); tip of embolus long, thin, scythe-like (Figs. 6, 7); posteriorly-directed epigynal plate usually wider than long, U-shaped and extending at most to the midpoint of the spermathecae (Fig. 8) . . . .*pearcei*

TAXONOMY

Neoanagraphis Gertsch & Mulaik 1936
Figures 1, 10

Neoanagraphis Gertsch & Mulaik 1936: 11 (Gnaphosidae); Gertsch 1941: 19 (Clubionidae); Comstock 1948: 327 (Gnaphosidae); Roewer 1955: 559 (Clubionidae, Liocraninae, Liocraneae); Bonnet 1958: 3046 (Drassidae); Lehtinen 1967: 251 (Clubionidae *sensu* str.); Brignoli 1983: 549 (Clubionidae, Clubioninae); Platnick 1993: 605 (Clubionidae); Platnick 1998: 701 (Clubionidae)

Type species.—*Neoanagraphis chamberlini* Gertsch & Mulaik 1936 by original designation.

Diagnosis.—Whether one considers *Neoanagraphis* spiders in the broad sense of all the genera formerly housed in the Clubionidae or in the Liocranidae, they can be distinguished from other North American genera in either family by the long tarsal claws on legs III and IV that appear almost devoid of teeth.

Description.—Small to medium-sized spiders, with no bodily pigmentation. Coloration of few live specimens examined similar to those preserved in alcohol: cephalothorax uniformly pale orange to tan-orange, darkening anteriorly, width about ⅔ of length, widest at legs II-III, males slightly wider than females, covered with thin, white hairs with scattered, dark, anteriorly or medially directed setae. Longitudinal row of single, anteriorly-directed setae between eyes and thoracic furrow. Eyes subequal surrounded by black rings. AER recurved in dorsal view, slightly procurved in anterior view, eyes separated by less than eye diameter. AME dull but not black, all others luminescent. PER straight to slightly recurved in dorsal view, procurved in anterior view, PLE separated from PME by eye diameter, PME slightly farther from each other. PER slightly longer than AER with PLE extended laterally just beyond ALE. Clypeus about height of eye diameter. Undivided chilum. Conspicuous longitudinal thoracic furrow. Chelicerae dusky orange, darker than cephalothorax. Teeth: 3 promargin, 2 retromargin, latter separated by 3× width of tooth base. Conspicuous boss. Endites quadrate, labium slightly wider than long. Sternum slightly longer than wide, sometimes darker than legs. Coxa similar in color to legs. Pre-coxal triangles lacking. Trochanters notched, III and IV deeply so. Legs similar in color to cephalothorax with heavy spination. Leg IV longest, about 15–40% longer than legs I-III which are all subequal in length with minute plumose or feathery hairs. Tarsi lacking claw tufts, dense with white scopulae, sometimes appearing flexible in preserved specimens. Tarsal claws of posterior legs extremely long with few teeth at base, almost hidden (Fig. 1). Tarsal claws of anterior legs shorter, looking more typical. Trichobothria on tarsi and metatarsi of varying lengths, some very long. Spination

pattern virtually non-varying for dorsal femora and ventral metatarsi; retrolateral surfaces show greatest variation (patterns that differ between genders/species listed separately under species descriptions). Some spines rest intermediate between two surfaces; these were consistently assigned to one surface although they readily could have been assigned to another. Patterns that were most consistent between both sexes and both species are: femora: I, II p0-1-1 or 0-1-1-1; I–IV d1-1-1; tibiae: III p1-1-1, d1-0-1, v2-2-2, IV p1-1-1, d1-0-1, v2-2-2; metatarsi: I v2-2-0, II v2-2-0, III p1-1-0-2, r1-1-0-2, v2-2-2, IV p1-1-0-2, d1-1-0, r1-1-0-2, v2-2-2. Abdomen uniformly cream to tan, in rare instances brown, with scattered dark setae, no conspicuous markings, many long setae on anterior surface, oval in shape, width about ⅔ of length in well-preserved specimens. Occasionally heart can be seen through dorsal integument. In gross examination, ALS occasionally very long appearing gnaphosoid in character in preserved specimens otherwise appearing short and conical. Embolus of male palp dorsally projecting on apical-most portion of tegulum, membranous conductor dorsal to embolus. Median apophysis on retrolateral surface of tegulum above midline, translucent, elongate and concave. Epigynum with median plate, posteriorly-directed spines lateral where epigynal plate originates anteriorly. Anterior epigynal openings sometimes not readily visible. In dorsal view, epigynum with two simple oval spermathecae, each with duct arching anteriolaterally to small rotund structure (bursa copulatrix?).

Natural history.—*Neoanagraphis* spiders have been collected in an unidentified mammal burrow (Ryckman & Lee 1956), in a tarantula (*Aphonopelma* sp.) burrow and in a kangaroo rat mound; but otherwise, little is known of their natural history. Several collection labels mention that the spiders were found on sand dunes or in washes; one male was live-collected as it crawled around a sandy wash around midnight, at 4 °C. They have been collected often at elevations of 900–1950 m; however, some were taken from below sea level near the Salton Sea to 200 m in Mexico and western Arizona. Jung and Roth (1974) listed it as being found in Zone 1 of their study which is characterized by limestone foothills, alluvial plains and valleys of the Chiracahua Mountains from 4000–5000 feet (1200–1500 m).

Only a few live specimens were captured during the course of this study. A female was maintained for >8 mon. She fed on *Drosophila* flies and small crickets but ignored mosquitoes, larval waxmoth (*Galleria mellonella*) and a spider (*Drassyllus insularis* Banks 1900).

Genitalic variation.—In this study, approximately 24 mature females of each species were available for examination. Despite fewer females relative to males, females showed greater genitalic variation. In both species, the epigyna are covered with hairs which obscure some of its minute features. The epigynal plate in *N. chamberlini* varied in length such that it could extend past the posterior edge of the underlying spermathecae or sometimes would just barely reach the posterior edge. Additionally, although the plate was usually V-shaped, the width of the plate varied from narrow to wide, and sometimes was rounded on the posterior edge (Fig. 5) similar to *N. pearcei*. The plate in *N. pearcei* was comparatively less variable in length, width and its rounded, U-shaped posterior edge (Fig. 8), however, at least one specimen had a V-shaped plate reminiscent of *N. chamberlini*. The lateral spurs were rather consistent in size within each species (conspicuous in *N. chamberlini*, minute in *N. pearcei*) and for the few specimens examined here that is a good diagnostic feature to be used in concert with other features such as anterior tibial spination. Yet they did vary from spike-like to that of an equilateral triangle and could be slightly different in form on the right and left sides of the same spider.

About half of the females of each species were dissected to inspect the dorsal view of the genitalia, leaving the other females intact for future researchers. There are no consistent internal characters that allow species separation. The small anterior rotund structures (bursa copulatrix?) for both species may lie directly on top of the spermathecae or extend laterally (Fig. 9). Likewise, the duct running to it may be thin or thick, and at an acute or obtuse angle of curvature. Possibly with greater numbers of spiders in the future, diagnostic internal features may become apparent.

In contrast, the males were very consistent in their palpal features with little marked var-
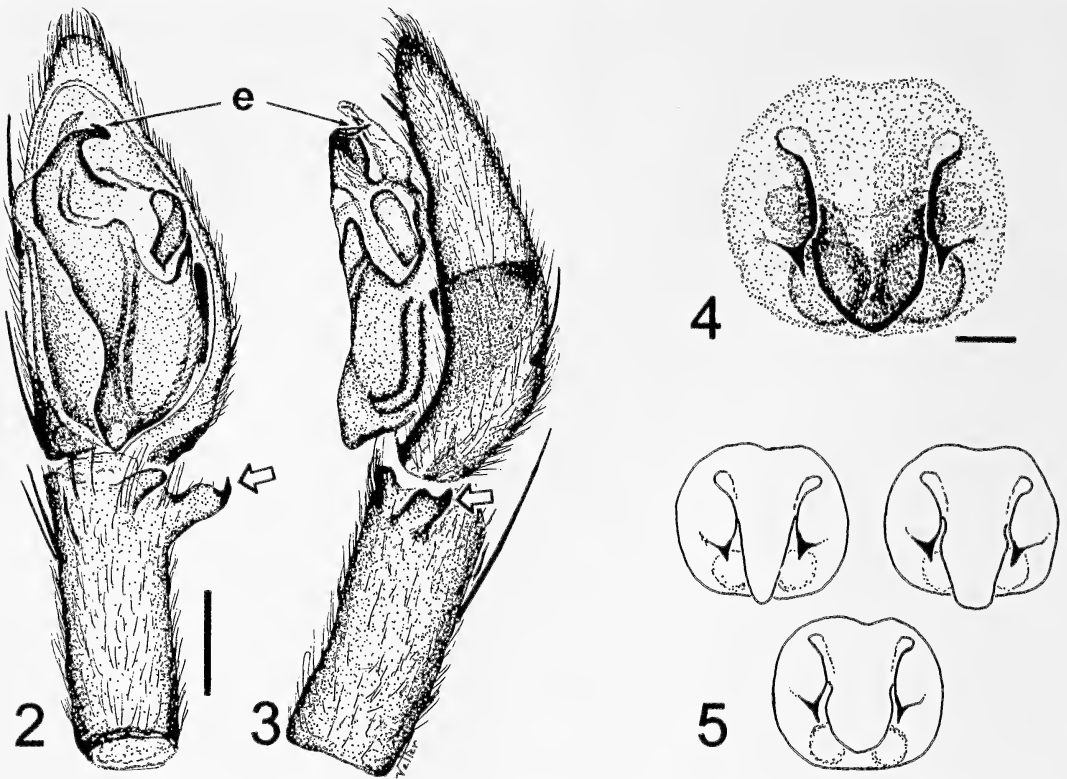
Figures 2–5.—*Neoanagraphis chamberlini* Gertsch & Mulaik. 2. Male left palp, ventral view; 3. Same, retrolateral view (scale = 0.25 mm); 4. Epigynum, ventral view, hairs removed from ventral surface (scale = 0.1 mm); 5. Schematic drawings of epigyna showing variation of epigynal plate and its position relative to the spermathecae. "e" = dorsally-directed embolus, additional arrows point to dorsal process of retrolateral tibial apophysis.

iation in characters except for differences due to aberrations caused by preservatives which expanded the palp or changed the relative orientation of the structures.

Neoanagraphis chamberlini Gertsch & Mulaik 1936
Figs. 2–5, 10

Neoanagraphis chamberlini Gertsch & Mulaik 1936: 11–12, fig. 15. Male holotype - White Sands, New Mexico, August 1934, in AMNH, examined.

Diagnosis.—The two species in the genus differ consistently in a number of traits and can be readily separated. *Neoanagraphis chamberlini* is characterized by (1) anterior tibia with two pairs of ventral spines (discounting smaller apicals if present), (2) the dorsal process of the retrolateral tibial apophysis (RTA) is thick and projected laterally (Fig. 2), (3) the dorsally-projecting embolus

tip is truncate and looks like a folded flap or cresting wave (Fig. 3), and (4) the epigynal plate extends posteriorly past the midpoint, and most often to the posteriormost edge of the spermathecae (visible through the integument) or beyond (Fig. 4, 5). In contrast, *N. pearcei* has (1) anterior tibia with three pairs of ventral spines (discounting smaller apicals if present), (2) the RTA is forked with the dorsal process straight, thin and apically-directed (Fig. 7), (3) dorsally-projecting embolus is long, thin and scythe-like (Fig. 7), and (4) the epigynal plate extends posteriorly only to the middle of the spermathecae (Fig. 8). Although there is some overlap of the sizes, in general, the typical *N. chamberlini* is distinctly larger than the typical *N. pearcei*.

Description.—*Male:* Total length 6.9 (3.8–9.1). Carapace 3.4 (1.9–4.5) length, 2.7 (1.6–3.7) width. Abdomen 3.4 (1.8–4.9) length, 2.1 (1.1–3.0) width. Cymbium 1.08 (0.85–1.26)
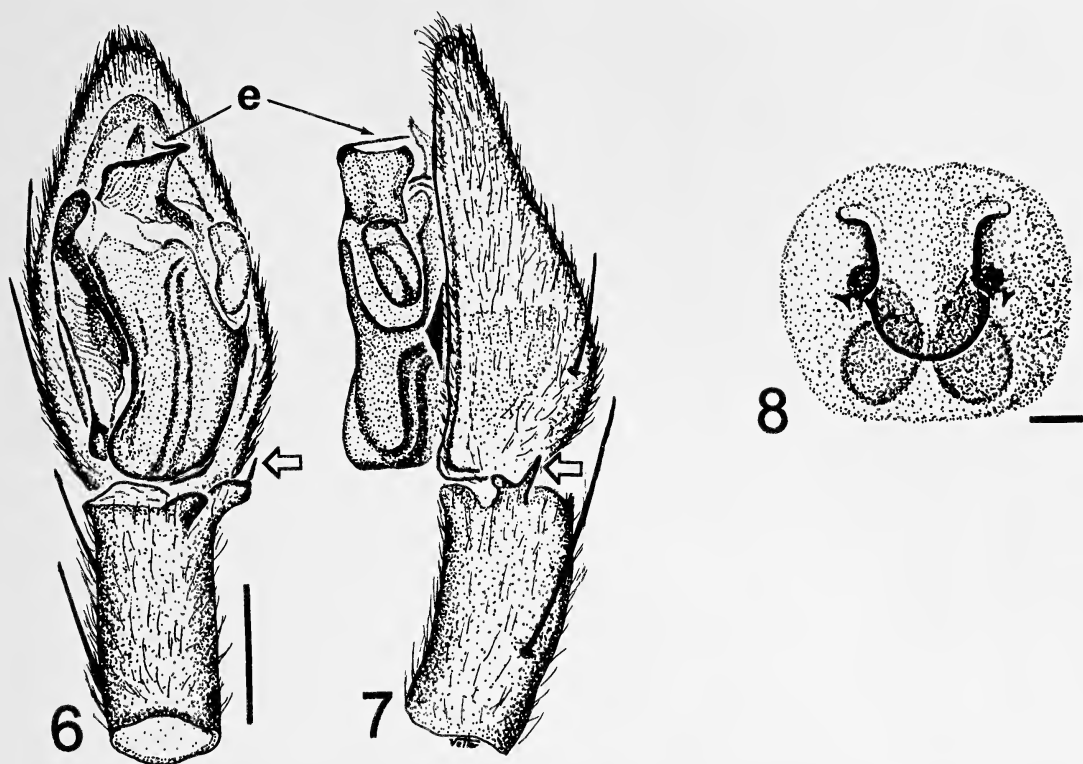
Figures 6–8.—*Neoanagraphis pearcei* Gertsch. 6. Male left palp, ventral view; 7. Same, retrolateral view (scale = 0.25 mm); 8. Epigynum, ventral view, hairs removed from ventral surface (scale = 0.1 mm). "e" = dorsally-directed embolus, additional arrows point to dorsal process of retrolateral tibial apophysis.

length. Additional spination differing from that presented for genus: femora: I r 0-1-1-1, II r 0-1-1 or 0-1-1-1, III p 0-1-1-0-1 or 1-1-1-1, IV p 0-1-1-0-1, r 0-1-1 or 0-1-1-0-1; tibiae: I p (variable with 2 or 3 spines), v 2-2-(2) (apicals weak), II p 1-1-1, r (variable with 0 to 2 spines), v 2-2-(2) (apicals weak), III r 0-1-1 or 1-0-1, IV r 1-0-1 or 1-1-0-1; metatarsi: II p (variable with 0 to 2 spines), d 1-1-0.

Female: Total length 7.7 (5.5–9.7). Carapace 3.6 (2.9–4.5) length, 2.8 (2.2–3.6) width. Abdomen 4.1 (2.3–5.7) length, 2.5 (1.3–3.8) width. Epigynal plate: 0.20 (0.14–0.24) for both length and width. Epigynal plate bordered anteriolaterally by conspicuous, posteriorly-directed spurs varying in shape from sharp spike to equilateral triangle. At posterior edge, plate varying from smoothly rounded U-shape (rare) to sharp, narrow V-shape (common); if extends posteriorly, plate more likely to be V-shaped. Spination as in male except for: femora: I d 1-1-0-1, II d 1-1-0-1, III r 0-1-1; tibiae: I p (variable with 0 to 2 spines).

Distribution.—From the mountains around the Central Valley through the southeastern deserts in California, into southern Nevada, the southern half of Arizona, New Mexico and the western edge of Texas (Fig. 10). Also in the state of Sonora in Mexico.

Material examined.—Holotype male, 112♂21♀, 46 immatures. **MEXICO:** *Sonora:* 5 mi. N. Hermosillo, near sea level, in unidentified rodent burrow, 16 April 1952, 1♀, R. Ryckman & K. Arakawa (AMNH), S. end Sonoita River, 26 November 1959, 1♂, V. Roth (AMNH). **UNITED STATES: Arizona:** *Cochise County:* Portal, 4800 feet, 8 August 1965, 1 imm., W. Gertsch (AMNH); 13.5 mi S. Apache, 4330 feet, in kangaroo rat mound, 8 September 1968, 1♂, 1 imm., E. Moore & T. Walker (VDR), 5 mi. N. Portal, 4770 feet, 19 April 1977, 1♀, R. Chew (VDR); Chiricahua Mountains, Southwest Research Station, 5400 feet, 16 September 1985, 1♂, V. Roth (CAS). *Graham County:* Calva, 3500 feet, 3 November 1955, 1♀, V. Roth (AMNH). *Pima County:* Organ Pipe Cactus National Monument, 1700 feet, on restroom floor, 18 November 1989, 1♂, W. Icenogle & T. Prentice (WRI); Tuc-
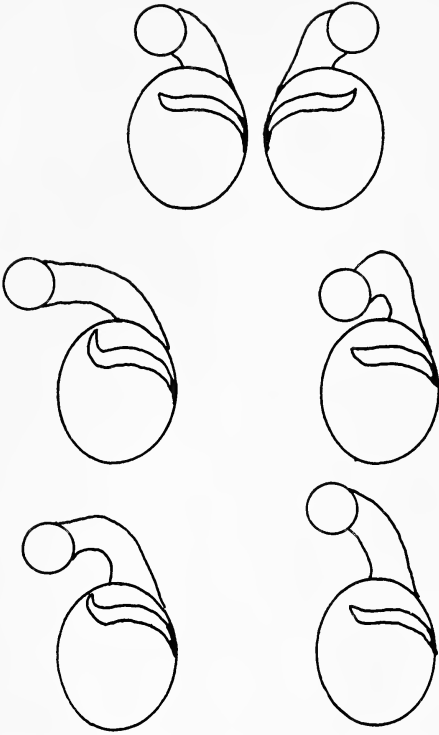
Figure 9.—Schematic drawings of the dorsal view of female *Neoanagraphis* genitalia. The top figure is the most common configuration of paired structures for both species. The remaining four figures show the variation among individuals with only one side drawn.

Figure 10.—Southwestern United States and northern Mexico. Distribution of *Neoanagraphis chamberlini* (○) and *N. pearcei* (●).

son, 2400 feet, 8 October 1953, 1♂, M. Cazier (AMNH), no date, 1♂, O. Bryant (AMNH). *Yavapai County:* Congress, 3000 feet, 8 August 1948, 1 imm., C. & P. Laurie (AMNH). *Yuma County:* Cabeza Prieta National Wildlife Refuge, Tule Well, 600 feet, pitfall traps, 9 November 1996, 3♂, V. Roth & D. Richman (NMSU); **California:** *Fresno County:* N. Kettleman Hills, under boards, 8 December 1993, 1♀, W.H. Tyson (CDFA). *Imperial County:* 1 mi W Harper's Well, San Felipe Creek, −100 feet, in dunes, probably 11 July 1968 (not 7 November), 1 imm., M.E. Irwin & P.A. Rauch (UCR); 3 mi NW Glamis, sand dunes, 4 March 1972, 1♀, A.R. Hardy (UCR). *Inyo County:* China Lake Naval Air Weapons Station, near S. Coso Village, 5800 feet, 27 May–8 June 1996, 1♀; 22 June–10 August 1996, 1 penult. ♀; in wash, 9 June–10 August 1996, 3 imm.; near Birchum Springs, 16 August–14 September 1996, 1♂; 22 June–10 August 1996, 1♂; White Hills, in pitfall trap under Joshua trees, 10 August–14 September 1996, 3♂; 4 mi N Flight Line & GI roads, 14 September 1996–15 February 1997, 1♀, G. Pratt & C. Pierce (UCR). *Kern County:* E. Randsburg, 12 April 1968, 1 imm.,

J. Cherry (UCR), Edwards Air Force Base, Leuman Ridge, 23 November 1997, in pitfall under *Larrea tridentata,* 1♂, C. & M. Breidenbaugh (UCR). *Riverside County:* Rice Dunes, 25 February 1978, 1♀, F. Andrews & A. Hardy (CDFA). *San Bernardino County:* Cadiz Dunes, 25 April 1978, 1 imm., A. Hardy & F. Andrews (CDFA); Joshua Tree National Monument, Cow Camp, 5800 feet, in pitfall traps, 24 September 1994, 5♂, W. Sakai (UCR); Twentynine Palms, October 1944, 1♂, J. Branch (AMNH). **Nevada:** *Nye County:* Nevada Test Site (see below), 61♂5♀, 35 imm., D. Allred (AMNH). **New Mexico:** *Bernalillo County:* Albuquerque, Indian Petroglyph State Park, 5000 feet, 7 June 1995, 1♂, summer 1996, 1♂, D. Lightfoot (UCR). *Doña Ana County:* Jornada Experimental Range, 4300 feet, in lowland grass pasture, 21 October 1999, 1♂, D. Richman (NMSU). *Otero County:* White Sands, August 1934, 1♂ (holotype), S. Mulaik (AMNH). *Socorro County:* 20 mi N Socorro, 4500–6500 feet, 1989–1992, 26♂7♀, 1 imm., S. Brantley (UCR). **Texas:** *Hudspeth County:* 8 mi. W. Sierra Blanca, 5 September 1946, 1♂ (AMNH). *Presidio County:* in nest of *Cratageomys castanops,* August 1948, 1♀, G. Menzies (AMNH).

Neoanagraphis pearcei Gertsch 1941
Figs. 6–8, 10

Neoanagraphis pearcei Gertsch, 1941: 19–20, fig. 46. Male holotype - Yermo, San Bernardino Co., California, 28 October 1939, in AMNH, examined.

Diagnosis.—See *N. chamberlini.*

Description.—*Male:* Total length 4.6 (3.2–6.8). Carapace 2.3 (1.7–3.0) length, 1.8 (1.3–2.6) width. Abdomen 2.4 (1.5–3.8) length, 1.4 (0.8–2.2) width. Cymbium 0.80 (0.49–1.02) length. Additional spination from that presented for genus: femora: I r 1-1-0-1, II r 1-

1-1 or 1-1-0-1, III r 0-1-1 or 1-1-1, IV r 0-1-1; tibiae: I p 1-1-0-1 or 1-1-1-1, r 1-1-1, v 2-2-2-(2) (apicals weak), II p 1-1-1-1, r 1-1-1, v 2-2-2-(2) (apicals weak), III r 0-1-1 or 1-1-1, IV r 1-1-1; metatarsi I p (variable with 0 to 2 spines), r 0-1-0 or none, II p 1-1-0, r 0-1-0, III d 0-1-0 or 1-1-0.

Female: Total length 6.0 (4.0–8.1). Carapace 2.8 (2.1–3.5) length, 2.2 (1.6–2.9) width. Abdomen 3.2 (1.8–4.8) length, 2.1 (1.2–2.9) width. Epigynal plate 0.15 (0.10–0.18) length, 0.24 (0.18–0.31) width. Epigynal plate bordered anteriolaterally by minute posteriorly-directed spurs; at posterior edge, plate typically rounded, U-shaped, extending only about to midpoint of underlying spermathecae (which can be seen through integument). Spination as in male except for: femora: I r (variable with 0 to 2 spines); tibiae: I p (variable with 0 to 3 spines), r none, II p 1-1-0-1, r none, IV r 0-1-1 or 1-1-1; metatarsi: II p none, r none, III d (variable from 1 to 3 spines).

Distribution.—Eastern Sierra Range south into the mountains surrounding the Coachella Valley in California, southern portions of Nevada and Utah, north and western Arizona (Fig. 10).

Material examined.—Holotype male, 86♂, 27♀, 25 imm. **UNITED STATES: Arizona:** *Mohave County:* 1 mi SE Bullhead City, 600 feet, pitfall trap, 22–26 December 1980, 1♂1♀, B. Phelps (CDFA); Virgin River, 3 mi N, 7 mi E Littlefield, in pitfall trap, March-October 1982, 1♀, D. Giuliani (CAS). *Yuma County:* near Sheep Tank Mine, 29 October 1958, 1♀, V. Roth (VDR). **California:** *Inyo County:* E. side Owens Lake, 17 September 1977, imm., F. Andrews & A. Hardy (CDFA); Eureka Valley, pitfall traps, November-December 1977, 2♂, February 1978, 1♀, April 1978, 1♀, D. Giuliani, A.R. Hardy & F.G. Andrews (CDFA); N. Eureka Valley, Inyo Mountains, Willow Springs Canyon, 3000–3600 feet, 29 September 1980–18 March 1981, 4♂; 6 mi E. Independence, 4600 feet, 6 December 1984–20 December 1986, 1♀; White Mountains, 5000 feet, 6 mi NE Big Pine, 25 April–22 July 1982, 1♀; 3 mi SW Big Pine, in pitfall, 6 October 1985–13 May 1986, 1♂; 1 mi W Big Pine, 4100 feet, October 1985–May 1986, 2♂, D. Giuliani (CAS); Death Valley National Monument, Scotty's Ranch at Travertine Springs, 2500 feet, 13 January 1981, 1♀, V. Roth (CAS); China Lake, Mt. Springs Canyon, 4500 feet, crawling on sand dune at night, 10 October 1997, 1♂, G. Pratt (UCR). *Mono County:* 9 mi N Bishop, Fish Slough, 4200 feet, sand dunes, 9 June–9 August 1987, 1♀, D. Giuliani (CAS). *Riverside County:* Joshua Tree National Monument, pitfall traps, Fried Liver Wash, 30 October 1965, 1♂; Quail Guzzler, 29–30 October 1965, 2♂; Pinyon Wells, 11 November 1965, 1♂; 0.7 mi S. Squaw Tank, no date, 1♂; Pleasant Valley, 2 December 1966, 1♂; 30 October 1968, 1♂, E.L. Sleeper, S.L. Jenkins (JLO); Boyd Desert Research Center, Coyote Creek, 3.5 mi S Palm Desert, pitfall trap, 10 May 1975, 1♀, W. Icenogle (WRI); Santa Rosa Mountains, Deep Canyon, 0.5 mi S junction Hwy 74 & Pinyon Crest turnoff, 3600 feet, in *Aphonopelma* burrow, 22 July 1976, 1♂1♀ (collected as immatures, matured late August), W. Icenogle (WRI); Cactus City, 10 mi W Chiriaco Summit off I-10, 1300 feet, in pitfall trap in wash, 29 April 1999, 1♀, 18 December 1999, 1♂1♀, R. Vetter (UCR). *San Bernardino County:* Yermo, 28 October 1939, 1♂ (holotype), W.M. Pearce (AMNH); Fort Irwin, Avawatz Mountains, 6150 feet, 22 May–17 June 1996, 1♀, G. Pratt & C. Pierce (UCR), 4250 feet, 26 May 1997, 1 imm., G. Pratt, W. Savary & D. Ubick (CAS); Pisgah Lava Flats, 24 May 1960, 1♂, B. Banta (CAS); Pisgah Crater, 11 February 1961, 2♀; 11 March 1961, 1♀; 12 April 1961, 1♀; 11 November 1961, 2♂1♀; 19 November 1962, 1♂, Norris & Heath (AMNH). **Nevada:** *Nye County:* Nevada Test Site (see below), 62♂7♀, 23 imm., Allred et al.(AMNH); Monitor Summit, 3 mi N, 17 E Tonopah, 6400 feet, March–October 1982, 1♂, D. Giuliani (CAS). **Utah:** *Washington County:* 10 mi N St. George, 21 July 1952, 1♀, M. Cazier, W. Gertsch, Schrammel (AMNH). Additional locales presented in Fig. 10 are listed in Allred & Gertsch (1976) and Allred & Kaston (1983) but material was not examined. **Utah:** *Kane County:* Nipple Bench, Smoky Mountain, Ahlstrom Point.

NEVADA TEST SITE

In 1960–1961 a comprehensive faunal survey was undertaken (Allred et al. 1963a) to inventory the animal diversity at the Nevada Test Site where atomic bombs were detonated in the 1940's. Twenty different collection techniques were employed; the fauna collected consisted of invertebrates (insects, arachnids, chilopods, millipedes) and vertebrates (reptiles, birds, rodents, carnivores, rabbits, artiodactyls); sampling occurred year-round. The survey encompassed about 3367 km² with exhaustive collection arrays differentiated by the dominant plant species. Inventory results are reported in Allred et al. (1963a) while the cryptic locale data (e.g., each spider label had Mercury, Nevada as the collection locale with a designation such as "4AA5C") was decoded by using the depository amendment (Allred et al. 1963b).
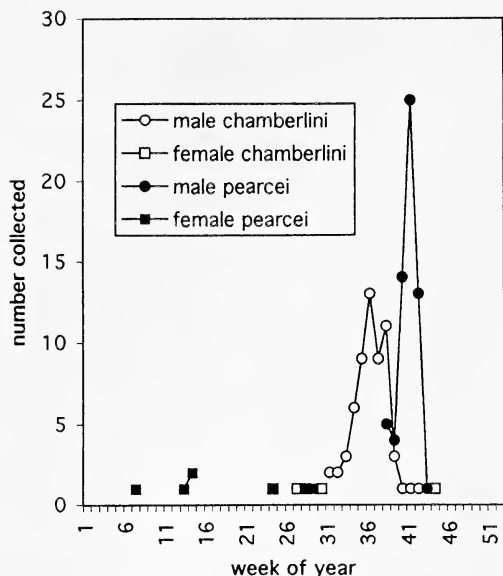
Figure 11.—Seasonal collection phenology of *Neoanagraphis chamberlini* (○) and *N. pearcei* (●) at the Nevada Test Site, Nye County, Nevada, 1960–1961.

Figure 12.—Comparison of cephalothorax lengths and widths of mature male *Neoanagraphis chamberlini* (○) and *N. pearcei* (●) from the Nevada Test Site, Nye County, Nevada, 1960–1961. (*n* = 58 for each species).

In the course of this revision, 62% (123 of 200) of the mature males and 61% (193 of 319) of all spiders examined were collected by Allred et al. (1963a) at NTS. Both species of *Neoanagraphis* were collected at NTS; specimens deposited at AMNH were about equally divided between the two species. Almost all *Neoanagraphis* spiders were collected in pitfall traps which explains the preponderance of males, most probably as they wandered in search of females. This affords a rather rare opportunity to examine characteristics between the two almost sympatric populations to compare traits where environmental conditions would be fairly similar.

Despite the fact that both species of *Neoanagraphis* spiders were collected within the NTS, there are striking differences between them. The temporal collection profiles show little overlap in phenology. Mature males of *N. chamberlini* were collected most often from mid-August until late September, and mature males of *N. pearcei* were collected from mid-September to late October (Fig. 11). (Specimens collected outside of NTS corroborate this phenology.) Despite being congenerics, there was an almost dichotomous separation in size as measured by the cephalothorax length and width of mature

males; only two very small *N. chamberlini* overlapped with the size range of *N. pearcei* (Fig. 12). (Specimens collected outside of NTS show similar patterns but with greater overlap (data not shown)). The two species also showed habitat differences in that *N. chamberlini* preferred the flat terrain of Yucca Flats which consisted of communities of *Coleogyne, Grayia-Lycium, Atriplex-Kochia* and thistle (i.e., tumbleweed, *Salsola kali*). In comparison, *N. pearcei* was found most often 15 km southward in the more montane sections of the NTS with a plant community strictly of creosote (*Larrea divaricata*) and *Franseria* sp.

Determination of immatures with spination.—Because mature specimens of the two *Neoanagraphis* species are readily differentiated by spination pattern and preferred distinctly different habitats at NTS, the NTS immatures were also examined to see if anterior tibia spination could be correlated with locale. Immature anterior ventral tibial spine pattern and cephalothorax length was recorded. Spination pattern was correlated to the coded locale data.

Immature spiders separated almost dichotomously into two groups with either 2 pairs or 3 pairs of anterior ventral tibial spines; there were a few immatures with 5 spines which were placed in the 3-pairs-of-spines group because spiders are more likely to add spines with age rather than lose them. (From

previous examination of mature specimens if there were supernumerary spines on *N. chamberlini* it usually was double the normal pattern, that is, 4 pairs of ventral tibial spines). When immature spination type was matched with locale data, the 2-pair-of-spines immatures (cephalothorax length: 0.93–3.67 mm) were found almost entirely in the flatland region (35 of 36) where *N. chamberlini* adults were most often found. The 3-pairs-of-spines immatures (cephalothorax length: 0.94–2.57 mm) were found almost exclusively in the mountain ranges (22 of 23) where adult *N. pearcei* was predominant.

With this evidence, it is reasonable to state that the spination aspect from the key above will successfully determine both species of *Neoanagraphis* spiders even as immatures. The generic characteristic of elongate tarsal claws III and IV is evident in the smallest spiders examined here. Therefore, even if one has disarticulated limbs and can verify a spiderling as *Neoanagraphis,* one can then identify it to species (unless additional species occur) by finding an anterior leg (which has a less elongate claw than the posterior legs) and examine spination pattern on the ventral tibial surface because it is the same for leg I and II.

Familial reassignment.—Specimens sent to AMNH were examined microscopically and with a scanning electron microscope. Dr. Norman Platnick has transferred the genus *Neoanagraphis* to the Liocranidae on the basis that the female has three cylindrical gland spigots on each posterior median spinneret and two on each posterior lateral spinneret (N.I. Platnick pers. comm.). Cylindrical (or tubuliform) glands, used in construction of eggsac silk, are lacking in the clubionids (Kovoor 1987). In addition, the male palpal structure of *Neoanagraphis* corresponds well with that of the liocranid genus *Agroeca* (N.I. Platnick pers. comm.) and other liocranids (J. Bosselaers pers. comm.).

Current keys.—The spider genus *Neoanagraphis* does not appear in any edition of Kaston's basic spider keys, *How to Know the Spiders* (Kaston 1953, 1972, 1978). In Roth (1993), under the Clubionidae, *N. pearcei* will properly key out to Group IV and then further to the *Neoanagraphis* couplet. In contrast, *N. chamberlini* does not key out correctly. At couplet 10, it gets shunted to Group III on the basis of its two pairs of ventral macrosetae.

Continuing through the Group III key, it will terminate at the *Agroeca* couplet or not key out at all depending upon one's degree of differentiation.

ACKNOWLEDGMENTS

LITERATURE CITED

Allred, D.M. & W.J. Gertsch. 1976. Spiders and scorpions from northern Arizona and southern Utah. Journal of Arachnology 3:87–99.

Allred, D.M. & B.J. Kaston. 1983. A list of Utah spiders with their localities. Great Basin Naturalist 43:494–522.

Allred, D.M., D.E. Beck & C.D. Jorgensen. 1963a. Biotic communities of the Nevada test site. Brigham Young University Science Bulletin, Biology Series 2(2):1–52.

Allred, D.M., D.E. Beck & C.D. Jorgensen. 1963b. Nevada test site study areas and specimen depositories. Brigham Young University Science Bulletin, Biology Series 2(4):1–15.

Banks, N. 1900. Some new North American spiders. Canadian Entomologist 32:96–102.

Bonnet, P. 1958. Bibliographia Araneorum. Tome II, 4me partie: N-S, Douladoure, Toulouse, Pp. 3027–4230.

Brignoli, P.M. 1983. A catalogue of the Araneae

described between 1940 and 1981. Manchester Univ. Press, Manchester, United Kingdom.

Comstock, J.H. 1948. The Spider Book. Cornell Univ. Press, Ithaca, New York.

Gertsch, W.J. 1941. New American spiders of the family Clubionidae. I. American Museum Novitates #1147, 20 pp.

Gertsch, W.J. & S. Mulaik. 1936. Diagnoses of new southern spiders. American Museum Novitates #851, 21 pp.

Jung, A.K.S. & V.D. Roth. 1974. Spiders of the Chiricahua mountain area, Cochise Co., Arizona. Journal of the Arizona Academy of Science 9: 29–34.

Kaston, B.J. 1953. How To Know The Spiders. Wm. C. Brown Company Publishers, Dubuque, Iowa.

Kaston, B.J. 1972. How To Know The Spiders. 2nd ed. Wm. C. Brown Company Publishers, Dubuque, Iowa.

Kaston, B.J. 1978. How To Know The Spiders. 3rd ed. Wm. C. Brown Company Publishers, Dubuque, Iowa.

Kovoor, J. 1987. Comparative structure and histochemistry of silk-producing organs in arachnids.

Pp. 160–186. *In* Ecophysiology of Spiders. (W. Nentwig, ed). Springer-Verlag, Berlin.

Lehtinen, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Annales Zoologici Fennici 4:199–468.

Platnick, N.I. 1993. Advances in Spider Taxonomy 1988–1991 With Synonymies and Transfers 1940–1980. New York Entomological Society, New York.

Platnick, N.I. 1998. Advances in Spider Taxonomy 1992–1995 with redescriptions 1940–1980. New York Entomological Society, New York.

Roewer, C.F. 1955. Katalog der Araneae, 2 Band, Abt. B. Institut Royal des Sciences Naturelles de Belgique, Brussels. Pp. 1–923.

Roth, V.D. 1993. Spider Genera of North America. 3rd ed. American Arachnological Society, Gainesville, Florida.

Ryckman, R.E. & R.D. Lee. 1956. Spiders and phalangids associated with mammals (*Citellus* and *Neotoma*) in southwestern United States and northern Mexico. Annals of the Entomological Society of America 49:406–409.

NOTES ON THE GENUS *SYBOTA* WITH A DESCRIPTION OF A NEW SPECIES FROM ARGENTINA (ARANEAE, ULOBORIDAE)

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ABSTRACT. *Sybota atlantica* new species is described from the Atlantic coast of Buenos Aires Province, Argentina. The morphology of genitalia and carapace suggests that the new species forms a monophyletic group with *S. mendozae* Opell 1979 and *S. rana* (Mello-Leitão 1941). The female genitalia of the genus shows an unusual grade of entelegyny, with copulatory and fertilization ducts leading to a common tube.

Keywords: Uloboridae, *Sybota,* taxonomy, Argentina

RESUMEN. *Sybota atlantica* nueva especie es descripta para la costa atlántica de la provincia de Buenos Aires, Argentina. La morfología genital y cefálica sugiere que la nueva especie forma un grupo monofilético con *S. mendozae* Opell 1979 y *S. rana* (Mello-Leitão 1941). Los órganos genitales femeninos muestran un inusual grado de enteleginia, con los conductos de copulación y fertilización convergiendo en un tubo común.

The genera of the family Uloboridae and their Neotropical species were revised by Opell (1979). In that work, he defined the genus *Sybota* Simon 1892 and included three species: *S. abdominalis* (Nicolet 1849) and *S. osornis* Opell 1979 from Chile, and *S. mendozae* Opell 1979 from western Argentina. Females of the genus share with those of *Polenecia* Lehtinen 1967 an abdominal projection extending beyond the spinnerets (Figs. 1, 3; Opell 1979: figs. 51, 102, 110, 116). Nevertheless, this feature does not reflect a close relationship between both genera. According to Coddington (1990), *Sybota* is the sister group of the clade *Orinomana* (*Hyptiotes* + *Miagrammopes*), all united by having the posterior lateral eyes on conspicuous tubercles. *Sybota* males have a well-developed conductor and a median apophysis with two or three projections (Figs. 5–7; Opell 1979: figs. 6A, B).

In the present paper I describe a new species, *Sybota atlantica,* from specimens collected in the coast of Buenos Aires Province (courtesy of Martín J. Ramírez, MACN), which seems to be closely related with *S. mendozae* because some cephalic and genitalic features (see discussion). Here I also redescribe the holotype of *S. rana* (Mello-Leitão 1941) from Salta province, a species not included in the Opell's revision, and describe details of its genitalia, an aspect omitted in the original description (Fig. 11). Although *S. rana* is known from only a poorly-preserved specimen, apparently collected during the molting process, it can be placed close to the other two species.

The homology of the tegular sclerites of the male palps of the Uloboridae is still unclear. Coddington (1990) suggested that the terms median apophysis and conductor, as identified by Opell, should be switched. Nevertheless I maintained Opell's names only to ease comparison with previously described species.

METHODS

Specimens are deposited in the following institutions: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN, Cristina L. Scioscia), Museo de La Plata (MLP, Luis Pereira), and Instituto Argentino de Investigaciones de las Zonas Aridas, Mendoza (IADIZA, Sergio Roig Juñent). The format of descriptions follows Opell (1979). The abbreviations are: C = conductor; CD = copulatory duct; CO = copulatory opening; CY = cymbium; E = embolus; FD = fertilization duct; MA = median apophysis; PP = posterior plate; S = spermathecae; ST = subtegulum; T = tegulum. Abbreviations
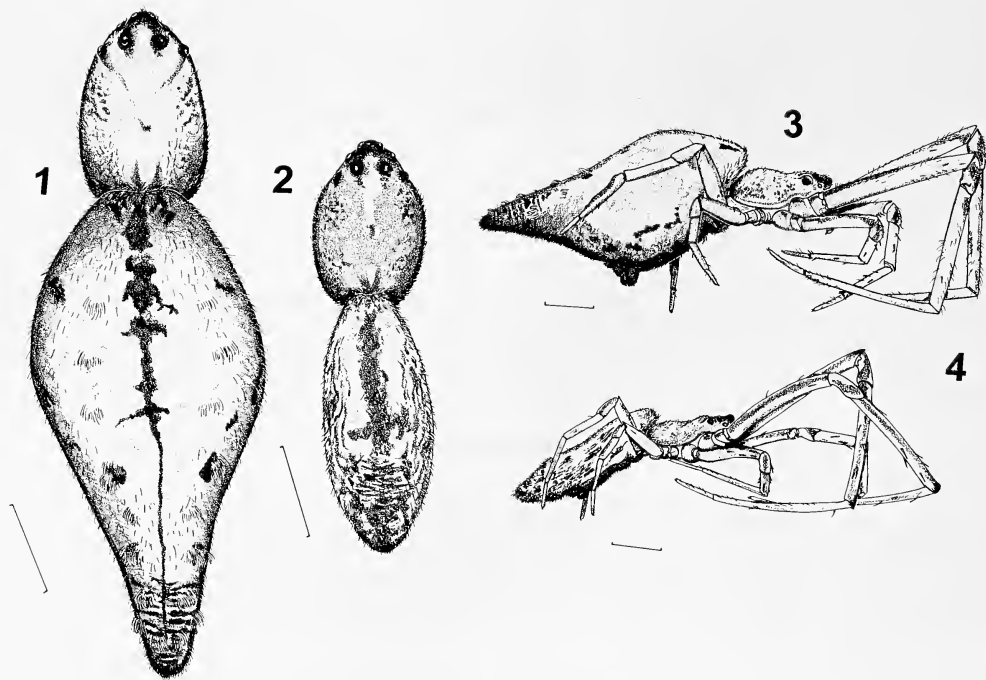
Figures 1–4.—**Sybota atlantica** new species. 1. Female, dorsal view; 2. Male, dorsal view; 3. Female, lateral view; 4. Male, lateral view (palps omitted). Scale bars = 1 mm.

for eyes are standard for the Araneae. The female genitalia were cleared with clove oil and observed with compound microscope. Measurements are expressed in millimeters.

Sybota atlantica new species
Figs. 1–10

Types.—Male holotype, and four female paratypes from Argentina, Buenos Aires Province, Mar del Tuyú, 2 May 1981, M.J. Ramírez (MACN No. 9639, 9640 and 9641, respectively).

Etymology.—The specific name refers to the type locality, on the Atlantic Coast of Argentina.

Diagnosis.—Males differ from those of *S. abdominalis* and *S. osornis* by having a longer embolus and conductor (Figs. 5–7), and by having the AMEs on a conspicuous tubercle (Figs. 2, 4). Females resemble those of *S. mendozae* and *S. rana* by having an elongate carapace, the AMEs on a tubercle, and the convoluted copulatory ducts, but differ by the shape of the epigynum and spermathecae (Figs. 8–10).

Description.—*Male (holotype):* Total length 4.76, carapace length 1.72, sternum length 1.08. Leg I: femur length 3.32, tibia length 3.04, metatarsus length 3.56, tarsus length 0.96. Carapace brown with yellowish median area between median eyes and fovea, margins with diffuse dark dots, more apparent on anterior region. Eyes bordered by dark rings. Sternum dark brown with a reddish median stripe. Legs same color as carapace but with tenuous, darker, longitudinal dorsal bands. Abdomen dorsally whitish with a gray longitudinal band (Fig. 2). Sides of the abdomen with diffuse longitudinal bands (Fig. 4). Venter pale reddish with a dark central band between pedicel and spinnerets. Palp: Femur with an excavated area where the bulb presumably fits (Fig. 5), tibia with a prolateral translucent prolongation (Fig. 7) covering partially the base of cymbium, which has a retrolateral basal tubercle (Fig. 5, arrow). Copulatory bulb: retrolateral surface of tegulum with a translucent membrane (Fig. 5); median apophysis with one basal and three distal projections (Figs. 5, 6); conductor long with two prongs: the proximal digitiform and the terminal flattened; embolus long, with tip fitting into the terminal prong of conductor.
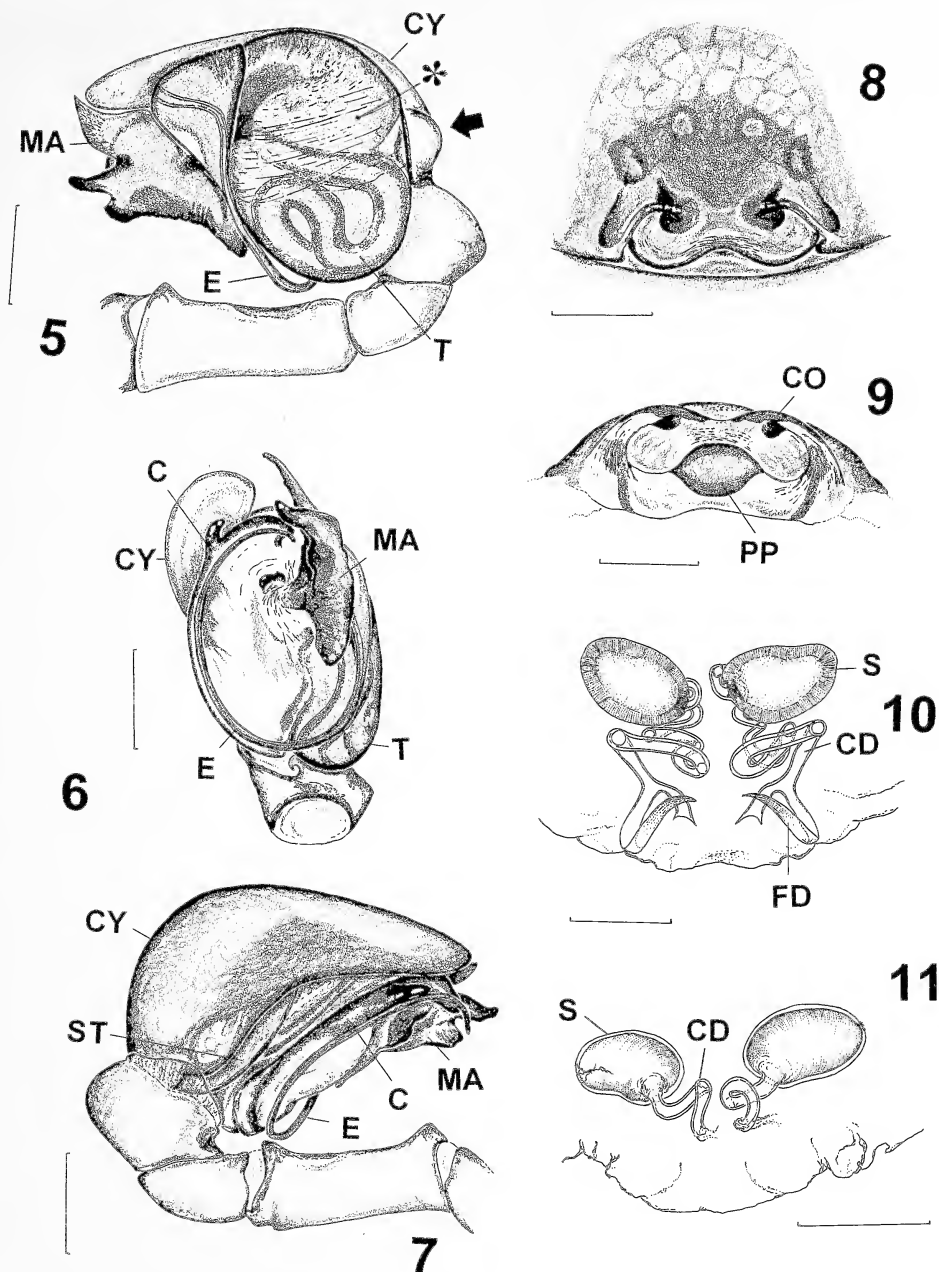
Figures 5–11.—Genitalia of *Sybota. 5–10. Sybota atlantica* new species. 5. Left male palp, retrolateral (arrow: cymbial tubercle; asterisk: tegular membrane); 6. Same, ventral; 7. Same, prolateral; 8. Epigynum, ventral view; 9. Same, posterior view; 10. Same, cleared, dorsal view. 11. *Sybota rana* (Mello-Leitão), cleared epigynum, dorsal view. Scale bars = 0.2 mm.

Female (paratype): Total length 7.35, carapace length 2.00, sternum length 1.32. Leg I: femur length 3.20, tibia length 2.60, metatarsus length 2.96, tarsus length 0.80. Color: Carapace, legs and eyes as in male, but AME tubercle less pronounced; sternum as in male, but with a stripe restricted to the anterior half. Dorsum of abdomen yellowish with a gray longitudinal band, wider anteriorly and diffuse dark spots, more evident in caudal and lateral

areas; dorsal and dorsolateral surfaces with aligned bundles of long setae (Figs. 1, 3). Venter yellowish with a brown median stripe between epigastric furrow and spinnerets. Epigynum: Lateral lobes flattened with a wide posterior notch (Fig. 8), copulatory openings under two elevated anterolateral margins (Fig. 9). Copulatory and fertilization ducts leading to a common convoluted tube.

Natural history.—The specimens were collected in typical uloborid horizontal orb-webs on shrubs and other medium-sized plants near the sandy ground in Mar del Tuyú. The spiders rested with legs I and II extended anteriorly (Martín J. Ramírez pers. comm.).

Material examined.—Only the type series.

Sybota mendozae Opell 1979

Sybota mendozae Opell 1979: 496 (female holotype and three female paratypes from 7 km W of Mendoza, Argentina, collected in "chaparral" at an elevation of 1200 m, March-April 1958, B. Patterson col., in MCZ and AMNH, not examined.)

New record.—ARGENTINA: *Mendoza,* Divisadero Largo, 8 March 1993, Debandi and S. Roig col., 1 penultimate female (IADIZA). *Note:* Although this specimen is subadult, the internal genitalia are developed and almost identical to those illustrated by Opell (1979).

Sybota rana (Mello-Leitão 1941)
Fig. 11

Uloborus rana Mello Leitão 1941: 111 (holotype Nº14635 from Coronel Moldes, Salta, Argentina, in MLP, examined). Roewer 1954: 1344.
Sybota rana Lehtinen 1967: 266.

Diagnosis.—The female resembles those *S. mendozae* and *S. atlantica* by cephalic morphology and by the long copulatory ducts, but are distinguished by the reniform spermathecae (Fig. 11) and the dorsal design of abdomen.

Description.—*Female (holotype, poorly preserved):* Carapace length, *ca.* 1.46; abdomen length, 3.96; leg I, femur length 2.34, tibia length 1.74, metatarsus length 2.00, tarsus length 0.74. Color: carapace dark brown; legs same color but with light longitudinal areas; chelicerae lighter than carapace. Abdomen (Mello-Leitão 1941, fig. 10) light brown with a dorsal longitudinal dark band (wider in front), and two large dorsolateral spots. The caudal parallel lines figured by Mello-Leitão

are no longer evident, probably faded. Epigynum: The poor condition of the specimen makes it impossible to distinguish the main epigynal structures; internally, only the reniform spermathecae and the distal portion of copulatory ducts remain; the preserved portion of them suggests that they were long (Fig. 11).

Material examined.—Only the holotype.

DISCUSSION

Sybota atlantica, S. mendozae and *S. rana* differ from the Chilean species *S. abdominalis* and *S. osornis* by the longer carapace, with the anterior median eyes on a prominent tubercle, by the epigynum with a posterior notch, and by the smaller spermathecae, with long and convoluted copulatory ducts (Figs. 1, 8–11; Opell 1979: figs. 115–119). Given that these conditions are not present in other closely related uloborid genera, they seem to be synapomorphies of the three Argentine species. If long copulatory ducts are functionally correlated with long embolus, the males of *S. mendozae* and *S. rana,* which are still unknown, should also have a long embolus.

Although *Ponella* Opell 1979, some *Zosis* Walckenaer 1837 and some *Philoponella* Mello-Leitão 1917 (genera which are not closely related with *Sybota*) also have long and convoluted copulatory ducts (Muma & Gertsch 1964; Opell 1979, 1981), they differ from *Sybota* by being entelegynes (i.e., the copulatory ducts and fertilization ducts are separated), while *Sybota* presents an intermediate and peculiar grade of entelegyny: the fertilization ducts arise from the proximal part of the copulatory ducts, without a direct conection with spermathecae. As noted by Opell (1983), the Uloboridae show a great diversity in genital features and comprises members both haplogyne, entelegyne and some intermediate types.

The observation of the web of *S. atlantica* in the field, and the photograph of an undeterminated Chilean specimen showed in Figs. 12 and 13 (in American Museum of Natural History, not examined), confirm that these spiders rest with legs I and II anteriorly extended, and that they construct typical horizontal orb-webs, as mentioned by Opell (1984) based on a juvenile specimen photographed by Norman Platnick.

Figures 12–13.—*Sybota sp.* from Alto de Vilches, Talca, VIII Región, Chile. 12. Web; 13. Living specimen (photographs by Martín J. Ramírez).

LITERATURE CITED

Coddington, J.A. 1990. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496:1–52.

Lehtinen, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Annales Zoologica Fennici 4:199–468.

Mello-Leitão, C.F. 1941. Las arañas de Córdoba, La Rioja, Catamarca, Tucumán, Salta y Jujuy, colectadas por los profesores Birabén. Revista del Museo de la Plata, Seccion Zoologia 2:12, 99–198.

Muma, M.M. & W. Gertsch. 1964. The spider family Uloboridae in North America north of Mexico. American Museum Novitates 2196:1–43.

Nicolet, H. 1849. Arácnidos. *In* Historia fís. y polít. de Chile. (C. Gay, ed.). Zoología III:319–543.

Opell, B.D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bulletin of the Museum of Comparative Zoology 148:443–549.

Opell, B.D. 1981. New Central and South American Uloboridae (Arachnida, Araneae). Bulletin of the American Museum of Natural History 170: 219–228.

Opell, B.D. 1983. The female genitalia of *Hyptiotes cavatus* (Araneae: Uloboridae). Transactions of the American Microscopical Society 102:97–104.

Opell, B.D. 1984. Comparison of carapace features in the family Uloboridae (Araneae). Journal of Arachnology 12:105–114.

Simon, E. 1892. Histoire Naturelle des Araignées, I. Paris.

OKILEUCAUGE SASAKII, A NEW GENUS AND SPECIES OF SPIDER FROM OKINAWAJIMA ISLAND, SOUTHWEST JAPAN (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. Several specimens of a unique spider were collected in Okinawajima Island, Southwestern Japan. They resemble the spiders of the genus *Leucauge* and its related genera. Phylogenetic analysis was performed to clarify the taxonomic position of the spider, which showed that the focal spider is a sister of a monophyletic group consisting of *Tylorida* and *Mesida.* Therefore it is described as a new genus and species under the name *Okileucauge sasakii* new species. This species lacks the rows of trichobothria on femur IV, which is the synapomorphy of the genera *Tylorida* and *Mesida.*

Keywords: *Okileucauge sasakii*, new genus, new species, Tetragnathidae

In the spring of 1997, I collected several specimens of a unique spider in Okinawajima Island, Southwestern Japan. This spider, hereafter called Okinawa spider, looked like a member of the genus *Leucauge* because it was hanging at the center of a horizontal orb-web and had a silver colored abdomen. The features of the male palpal organ, female epigynum and internal genitalia as well as general appearance show that the Okinawa spider is related to the genus *Leucauge.* However, the Okinawa spider lacks the rows of trichobothria on femur IV which is a conspicuous feature of the genus *Leucauge* and its related genera *Tylorida* and *Mesida.* On the other hand, American spiders of the genus *Metabus,* another related genus, also lack the rows of trichobothria on femur IV. I performed a phylogenetic analysis to clarify the relationship among these spiders. The cladogram shows that the Okinawa spider is a sister of a monophyletic group consisting of the genera *Tylorida* and *Mesida.* The cladogram also shows that *Leucauge* is a sister of the clade Okinawa + *Tylorida* + *Mesida* and that *Metabus* is a sister of the clade Okinawa + *Tylorida* + *Mesida* + *Leucauge.* These results led me to describe the new genus, though it is monotypic.

All the type specimens designated in this paper are deposited in the collection of the Zoological Department of National Science Museum, Tokyo (NSMT).

PHYLOGENETIC ANALYSIS

Methods.—*Taxa used in the analysis:* Spider in question from Okinawajima Island, *Tylorida striata* (Thorell 1877), *Mesida* sp. from Taiwan, *M. argentiopunctata* (Rainbow 1916), *Metabus gravidus* (O. Pickard-Cambridge 1899), *Leucauge subblanda* Bösenberg & Strand 1906, *L. argentina* (Hasselt 1882), *L. granulata* (Walckenaer 1841), *L.* sp. from New Guinea Island, *Metleucauge chikunii* Tanikawa 1992, *Meta nigridorsalis* Tanikawa 1994, *M. reticuroides* Yaginuma 1958, and *Nephila clavata* L. Koch 1878.

Nephila clavata was used as an out group judging from the cladogram made by Hormiga *et al.* (1995). Due to lack of the male specimen of *M. argentiopunctata,* the male characters of the species were judged from the figures made by Davies (1987) as far as possible.

Characters and character states: 1. Trichobothria on femur IV of female: none (0); less than 10 pairs (1); 10 pairs and over (2). 2. Depth of the thoracic groove of female: shallow, bottom visible from above (0); deep, bottom invisible from above (1). 3. Cheliceral teeth on posterior margin of fang furrow of female: 4 (0); 5 (1). 4. Booklung cover of female: partly grooved (0); smooth (1). 5. Color of abdomen of female: without silver color (0); with silver color (1). 6. Seminal receptacles of female: sclerotized (0); not sclerotized (1). 7. Clypeus height: smaller than one AME diameter (0); equal or larger than one AME
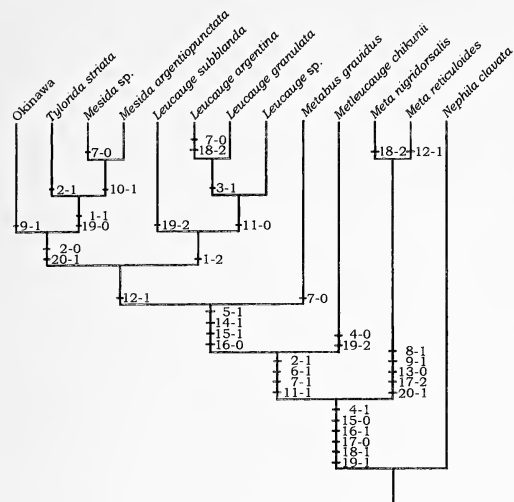
Figure 1.—Minimal length cladogram for the data matrix in Table 1. Length: 39; consistency index: 0.615; retention index: 0.712; rescaled consistency index: 0.438.

Figure 2.—*Okileucauge sasakii* new species, female on a leaf.

diameter. 8. Cheliceral size of the male versus that of the female: same (0); larger (1); smaller (2). 9. Large tooth or modified tooth on fang furrow of male chelicera: absent (0); present (1). 10. Spur on anterior surface of male chelicera: absent (0); present (1). 11. Projection of cymbium of male palp other than paracymbium: absent (0); present (1). 12. Lateral eyes of the male: separate (0); touching (1). 13. Course of reservoir within tegulum of male palp in ventral view: without switchback (0); with switchback (1). 14. Conductor of male palp: well sclerotized, black or dark brown (0); less sclerotized, almost colorless (1). 15. Conductor wraps embolus: absent (0); present (1). 16. Metine embolic apophysis: absent (0); present (1). 17. Paracymbium of male palp: small and finger shaped (0); small and flattened (1); large and modified (2). 18. Macrosetae on patella of male palp: 2 (0); 1 (1); none (2). 19. Length of tibia of male palp: short, tibia/patella less than 1.2 (0); long, tibia/patella 1.2 to 2.0 (1); very long, tibia/patella more than 2.0 (2). 20. Epigynum: well sclerotized (0); weakly sclerotized (1). The data matrix is shown in Table 1.

When Hormiga *et al.* (1995) made a phylogenetic analysis of tetragnathid spiders, 60 characters were used. Of these, 10 characters were also used in the present study (1, 4, 7, 8, 12, 13, 15, 16, 17, 18). The remaining char-

acters were not used because no data were available on the specimens used in the present study or they were uninformative.

Analysis: I used PAUP version. 3.1.1 (Swofford 1993) for the analysis. I used the branch and bound search method. I chose the ACCTRAN, accelerated transformation, for the character optimization. Multistate characters were treated as unordered.

Results.—As a result I obtained the cladogram shown in Fig. 1 (tree length 39; consistency index 0.615; retention index 0.712; rescaled consistency index 0.438). The cladogram shows that *Tylorida* is a sister of *Mesida,* the Okinawa spider is a sister of *Tylorida* + *Mesida,* and *Leucauge* is a sister of Okinawa + *Tylorida* + *Mesida,* and *Metabus* is a sister of Okinawa + *Tylorida* + *Mesida* + *Leucauge.* If the Okinawa spider were placed in any of these genera, that genus would not be a monophyletic group. Thus, I conclude that the new genus should be described for this spider.

DESCRIPTION

Family Tetragnathidae

Genus *Okileucauge* new genus

Type species.—*Okileucauge sasakii* new species by monotypy.

Diagnosis.—*Okileucauge* is a sister of the group consisting of genera *Tylorida* and *Mesida.* The synapomorphy of the latter group is the presence of rows of trichobothria on femur IV. That is, *Okileucauge* can be separated from the genera *Tylorida* and *Mesida* by the absence of rows of trichobothria on femur IV. The group *Okileucauge* + *Tylorida* + *Mesida* is a sister of *Leucauge.* The synapomorphies

Table 1.—Data matrix (Ok: spider in question from Okinawajima, Ty: *Tylorida striata*, Me1: *Mesida* sp., Me2: *Mesida argentiopunctata*, Mb: *Metabus gravidus*, Le1: *Leucauge subblanda*, Le2: *Leucauge argentina*, Le3: *Leucauge granulata*, Le4: *Leucauge* sp., Ml: *Metleucauge chikunii*, Mt1: *Meta nigridorsalis*, Mt2: *Meta leticuloides*, Ne: *Nephila vlavata*).

Character	Ok	Ty	Me1	Me2	Mb	Le1	Le2	Le3	Le4	Ml	Mt1	Mt2	Ne	States	Step	CI	RI	RC
1	0	1	1	1	0	2	2	2	2	0	0	0	0	3	2	1.00	1.00	1.00
2	0	1	0	0	1	1	1	1	1	1	0	0	0	2	3	0.33	0.60	0.20
3	0	0	0	0	0	0	1	1	0	0	0	0	0	2	1	1.00	1.00	1.00
4	1	1	1	1	1	1	1	1	1	0	1	1	0	2	2	0.50	0.00	0.00
5	1	1	1	1	1	1	1	1	1	0	0	0	0	2	1	1.00	1.00	1.00
6	1	1	1	1	?	1	?	1	1	1	0	0	0	2	4	0.25	0.40	0.10
7	1	1	0	1	0	1	0	1	1	1	0	0	0	2	1	1.00	1.00	1.00
8	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0.50	0.50	0.25
9	1	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0.50	0.50	0.25
10	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	1.00	1.00	1.00
11	1	1	1	1	1	1	1	1	1	1	0	0	0	2	2	0.50	0.80	0.40
12	1	1	1	?	0	1	1	1	1	0	0	1	0	2	2	0.50	0.67	0.33
13	1	1	1	1	1	1	1	1	1	1	0	0	1	2	1	1.00	1.00	1.00
14	1	1	1	1	1	1	1	1	1	0	0	0	0	2	1	1.00	1.00	1.00
15	1	1	0	0	0	0	0	0	0	1	1	1	1	2	2	0.50	0.50	0.25
16	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0.50	0.50	0.25
17	0	0	0	0	0	0	2	1	0	0	1	2	1	3	2	1.00	1.00	1.00
18	1	1	1	1	1	1	1	1	1	1	2	1	0	3	3	0.67	0.00	0.00
19	1	0	0	?	1	2	2	1	1	2	1	1	0	3	4	0.50	0.33	0.17
20	1	1	1	1	0	0	0	0	0	0	1	1	0	2	2	0.50	0.80	0.40
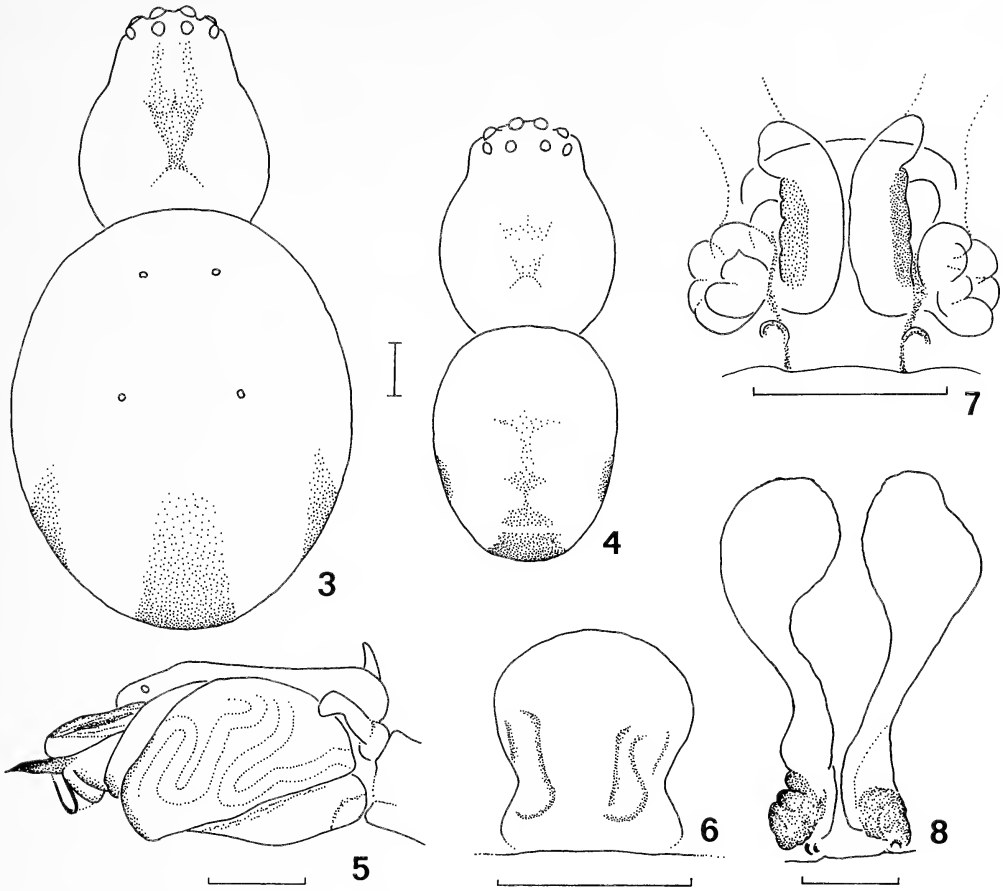
Figures. 3–8.—3, Female carapace and abdomen, dorsal view (holotype: NSMT—Ar 4301); 4, Male carapace and abdomen, dorsal view (paratype: NSMT—Ar 4305); 5, Male left palp, lateral view (paratype: NSMT—Ar 4305); 6, Epigynum (holotype: NSMT—Ar 4301); 7, Female genitalia, dorsal view; 8, Same, seminal receptacle expanded. (Scales: 0.25mm.)

of the former group are 1) shallow thoracic groove of female, 2) weakly sclerotized epigynum. The genera, *Okileucauge, Tylorida, Mesida, Leucauge,* and *Metabus* make a monophyletic group. The synapomorphies of the group are 1) abdomen having silver color; 2) conductor of male palp being weakly sclerotized, 3) conductor wraps embolus, 4) male palp lacks metine embolic apophysis.

Description.—Carapace longer than wide, median fovea shallow or bottom visible from above. Median ocular area almost as long as wide; slightly narrower in front than behind. Female chelicera with 3 promarginal and 4 retromarginal teeth on fang furrow; male chelicera with a big tooth at the innermost part of posterior margin of fang furrow. Male palp: course of reservoir within the tegulum switch-

backed; weakly sclerotized conductor wraps embolus. Labium wider than long. Sternum almost as long as wide. Abdomen longer than wide, with silver scales. Seminal receptacle not sclerotized. Booklung cover smooth.

Etymology.—Generic name is a coined word made from Okinawa, native island of the type species, and *Leucauge.* The name is feminine.

Okileucauge sasakii new species
(Figs. 2–8)

Specimens examined.—*Type series:* Holotype female, Kunigami-son, Okinawajima Island, Okinawa Pref., Japan, 1 April 1997, A. Tanikawa leg. (NSMT—Ar 4301). Paratypes: 2♀, same data except 30 March 1997 (NSMT—Ar 4302–4303), 1♀ 1♂, same data

except 1 April 1997 (NSMT—Ar 4304–4305), 2♀, same data except 2 April 1997 (NSMT—Ar 4306).

Other specimens examined: 3♀, Kunigami-son, Okinawajima Is., Okinawa Pref., Japan, 1 April 1997, A. Tanikawa leg. 1♀, same data except 2 April 1997.

Description.—[Based on the female holotype and the male paratype; variations among the specimens examined are given in the parentheses.] *Measurement* (in mm): Total length ♀ 3.10 (2.77–3.10), ♂ 2.18; carapace length ♀ 1.15 (1.08–1.16), ♂ 1.07; width ♀ 0.94 (0.92–0.96), ♂ 0.88; abdomen length ♀ 2.16 (1.61–2.16), ♂ 1.18, width ♀ 1.64 (1.27–1.64), ♂ 0.90. Length of legs (tarsus + metatarsus + tibia + patella + femur = total): ♀ holotype, I, 0.78 + 2.48 + 1.98 + 0.56 + 2.14 = 7.94, II, 0.65 + 1.83 + 1.48 + 0.51 + 1.75 = 6.22, III, 0.38 + 0.75 + 0.56 + 0.31 + 0.90 = 2.90, IV, 0.45 + 1.18 + 0.98 + 0.34 + 1.39 = 4.34. ♂ paratype, I, 0.74 + 2.40 + 2.09 + 0.51 + 2.11 = 7.85, II, 0.59 + 1.66 + 1.47 + 0.46 + 1.69 = 5.87, III, 0.34 + 0.64 + 0.53 + 0.27 + 0.80 = 2.58, IV, 0.40 + 1.03 + 0.87 + 0.27 + 1.23 = 3.80.

Female and male: Carapace length/width ♀ 1.22 (1.13–1.24), ♂ 1.22. Length of leg I/length of carapace ♀ 0.93 (0.88–1.00), ♂ 0.90. Male palp (Fig. 5): tibia with one macroseta; cymbium with a projection other than paracymbium; weakly sclerotized conductor wraps embolus; reservoir in tegulum switch-backed. Abdomen length/width ♀ 1.31 (1.12–1.31), ♂ 1.31. Female genitalia: epigynum simple and weakly sclerotized as in Fig. 6; seminal receptacles not sclerotized (Fig. 8).

Coloration and markings in alcohol: Female and male: Carapace yellow. Abdomen silver with black marking as in Figs. 2–4.

Range.—Japan (Northern part of Okinawajima Island).

Remarks.—The present new species looks like a small sized species of the genus *Leucauge* or its related genera *Tylorida* and *Mesida* in general appearance. However it can be easily separated from the latters by the absence of rows of trichobothria on femur IV.

Etymology.—The species is dedicated to Mr. Takeshi Sasaki, University Museum of the Ryukyus, who supported my field research in Okinawajima island.

LITERATURE CITED

Davies, V. T. 1988. An illustrated guide to the genera of orb-weaving spiders in Australia. Mem. Queensland Mus., 25:273–332.

Hormiga, G., W. G. Eberhard & J. A. Coddington. 1995. Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae, Tetragnathidae). Australian J. Zool., 43:313–364.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Ver. 3.1.1. Computer program distributed by Illinois State Natural History Survey, Champaign, Illinois.

REVISIÓN DE LAS ESPECIES DE
FREYA DEL GRUPO *DECORATA* (ARANEAE, SALTICIDAE)

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ABSTRACT.   Eight species of the genus *Freya* Koch 1846, closely related with the type species *Freya decorata* (Koch 1846), are revised and redescribed: *F. decorata, F. regia* (G. & E. Peckham 1896), *F. maculatipes* (Cambridge 1901), *F. nigrotaeniata* (Mello-Leitão 1945) new combination, *F. rubiginosa* (Koch 1846), new combination. The female of *F. nigrotaeniata* is described for the first time. Three new species are described: *F. dureti* from Brazil, *F. chapare* from Bolivia and *F. atures* from Venezuela. Diagnostic characters for the genus are given.

RESUMEN.   Ocho especies del género *Freya* Koch 1846, estrechamente relacionadas con la especie tipo *Freya decorata* (Koch 1846), son revisadas y redescriptas: *F. decorata* (Koch 1846), *F. regia* (G. & E. Peckham 1896), *F. maculatipes* (Cambridge 1901), *F. nigrotaeniata* (Mello-Leitão 1945) nueva combinación y *F. rubiginosa* (Koch 1846) nueva combinación. Las hembras de *F. nigrotaeniata* se describen por primera vez. Se describen tres especies nuevas: *F. dureti* de Brasil, *F. chapare* de Bolivia y *F. atures* de Venezuela. Se dan caracteres diagnósticos del género.

Keywords: Salticidae, *Freya decorata* group, Neotropica

C.L. Koch describió en 1846 veintitrés especies nuevas de Salticidae en el género *Euophrys* Koch 1834 de las cuales dieciséis proceden del área Neotrópica. Posteriormente (1850) creó trece nuevos subgéneros entre los que distribuyó estas especies, evidentemente disímiles. De los seis subgéneros que incluyen especies neotropicales, cuatro han sido elevados a la categoría de géneros: *Aphirape, Corythalia, Frigga* y *Freya* (que a su vez incluye a *Thore* como sinónimo) mientras que *Trivia* se considera sinónimo de *Euophrys*.

Veinte especies han sido descriptas como *Freya,* mientras que numerosas otras han sido incorporadas, transferidas desde otros géneros: cinco fueron descriptas originalmente como *Euophrys,* quince como *Cyrene* Peckham & Peckham 1893, una como *Eustiromastix* Simon 1902, una como *Phiale* Koch 1846, dos como *Attus* Walckenaer 1805 y tres como *Heraclea* G. & E. Peckham 1896. Con posteriores transferencias y sinonimias, el género *Freya* comprende en la actualidad veintisiete especies.

En este trabajo se trata un grupo de ocho especies, estrechamente relacionadas con *Freya decorata* (Koch 1846), especie tipo del género. La identificación de la especie tipo se ha hecho a lo largo de los años sobre la base de la descripción y dibujo originales, ya que no se ha podido hallar el material tipo, pese a que otros especímenes descriptos en la misma época por Koch se encuentran en buen estado en el Zoologisches Museum de Berlín.

Las especies del grupo decorata reúnen las siguientes características: 1) Quelíceros verticales, unidentados; 2) Palpo con apófisis tibial retrolateral gruesa, tuberosa, con una punta cónica dirigida hacia la cara ventral, el ápice o la base de la tibia (Figs. 8–13); 3) Embolo cónico, relativamente corto, recto o apenas curvado, acompañado por el conductor paralelo, membranoso, aproximadamente de la misma longitud que el émbolo (Figs. 19–31); 4) Epigino: placa limitada anteriormente por un surco curvo, carenado; borde posterior con bolsillos de anclaje; orificios de copulación relativamente pequeños, ubicados en la mitad anterior del epigino; espermatecas esféricas u ovoideas (Figs. 36–57); y 5) Opistosoma en ambos sexos con tres bandas dorsales longi-
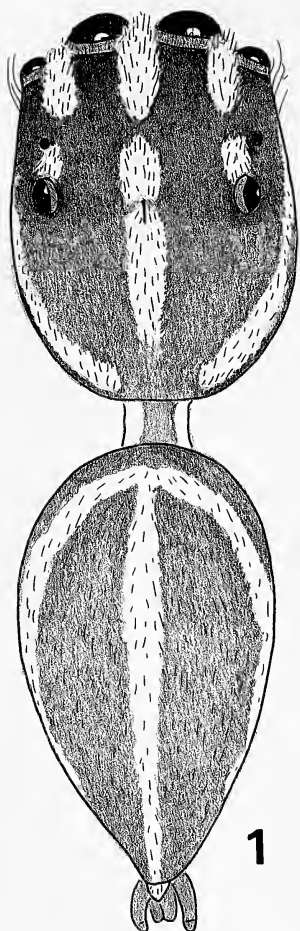
Figura 1.—*Freya decorata,* macho de Brasil, Pará, vista dorsal. Escala = 1 mm.

tudinales de pelos blancos; hembras con bandas radiantes oscuras en la región torácica (Fig. 1).

Algunos de estos caracteres aislados pueden encontrarse en otras especies de *Freya* o de otros géneros, pero teniendo en cuenta que un género se define por su especie tipo y que las ocho especies aquí tratadas reúnen los caracteres mencionados, deben considerarse como un grupo monofilético. Es posible que gran parte de las especies actualmente clasificadas como *Freya* deban ser excluidas. No existen suficientes estudios ni evidencias que indiquen las relaciones de *Freya* con otros géneros de Salticidae. Sólo futuras revisiones de otros grupos podrán aportar argumentos para discusiones filogenéticas.

El patrón de manchas y bandas es notablemente uniforme entre las especies del grupo aquí tratadas y algunas son simpátridas en el área de distribución. Las diferencias residen fundamentalmente en los caracteres de los órganos copuladores, algunos de los cuales no fueron advertidos por autores anteriores, como la presencia de un conductor paralelo al émbolo. La identificación que en el presente trabajo se hace de *Freya decorata* se basa en parte en el material de Guayana Francesa y Guyana estudiado por Caporiacco (1948, 1954) y el colectado por Galiano en Brasil, en los Estados de Pará (localidad tipo) y Amazonas. Algunas especies están representadas en las colecciones por material relativamente abundante, mientras que de otras se dispone de un único ejemplar. La identificación es posible cuando se trata de ejemplares machos, pero se hace dificultosa cuando se trata de hembras, debido a la gran uniformidad de los epiginos. En este trabajo, machos y hembras de cada especie se consideran coespecíficos cuando han sido colectados juntos en la misma localidad. Una decisión difícil es si *Freya rubiginosa* (Koch 1846) nueva combinación es una buena especie o solo una variante de *F. decorata.* En este trabajo se la considera como diferente, pese a haber sido colectada en Pará con machos y hembras de *F. decorata.* El hecho de que cuatro ejemplares coincidan totalmente con el holotipo hembra de *F. rubiginosa* y que se puedan distinguir de las que aquí se determinan como *F. decorata* justifica esta decisión.

MÉTODOS

El formato de las descripciones es según Galiano (1963b); la quetotaxia se describe como en Platnick y Shadab (1975) con pequeñas modificaciones. Todas las medidas se dan en milímetros.

Abreviaturas: OMA, OLA, OMP y OLP: ojos medios anteriores, laterales anteriores, medios posteriores y laterales posteriores, respectivamente; RC = región cefálica, RT = región torácica, E = émbolo, C = conductor, ATR = apófisis tibial retrolateral, BA = bolsillo de anclaje, CC = conducto de copulación, CF = conducto de fertilización, Es = espermateca, OC = orificio de copulación, ap = apical, b = basal, d = dorsal, p = prolateral, r = retrolateral, v = ventral, p.p. = pro parte, en parte. *Abreviaturas de los Museos*: Museo Argentino de Ciencias Naturales, Buenos Aires: MACN; Museum of Comparative

Zoology, Harvard: MCZ; Milwaukee Public Museum, Wisconsin: MPM; Zoologisches Museum, Berlín: ZMB; Museo Zoologico de "La Specola," Florencia: MLS; Natural History Museum, Londres: NHM;

Museo de La Plata, Argentina: MLP; Muséum National d'Histoire Naturelle, París: MNHN; Museu de Zoologia da Universidade de São Paulo, Brasil: MZSP; Museu Nacional de Rio de Janeiro, Brasil: MNRJ.

Género *Freya* C.L. Koch 1850

Euophrys (p.p.): C.L. Koch 1846: 200–203. Roewer 1954: 1698.

Freya C.L. Koch 1850: 66 (nuevo subgénero de *Euophrys*). Bonnet 1956: 1918. Simon 1864: 31; 1902: 412 (= *Heraclea*); 1903: 723, 730, 733, 739 (p.p.). Petrunkevitch 1911: 651 (p.p.); 1928: 198 (p.p.). Neave 1939: 422. Chickering 1946: 163 (p.p.). Galiano 1963a: 23; 1982: 53. Brignoli 1983: 639; 1985: 416. Platnick 1989: 562; 1993: 760; 1997: 884. Prószyński 1990: 138.

Heraclea Peckham & Peckham 1896: 78 (nuevo género). Neave 1939: 621.

Attus (p.p.) Taczanowski 1871: 70.

Cyrene Cambridge 1901: 222 (= *Heraclea*).

Thore C.L. Koch 1850: 66 (nuevo subgénero de *Euophrys*). Simon 1903: 730 (= *Freya*). Neave 1940: 477. Bonnet 1959: 4595 (= *Freya*).

Trivia (p.p.) C.L. Koch 1850: 66 (nuevo subgénero de *Euophrys*). Simon (p.p.) 1864: 314. Neave 1940: 572. Bonnet 1959: 4697 (= *Freya*).

Especie tipo.—*Euophrys decorata* C.L. Koch 1846.

Diagnosis.—Se diferencia de *Phiale* Koch 1846 y de *Euophrys* Koch 1834, por presentar en la división apical del tegulo, un conductor membranoso casi paralelo al émbolo, el cual es apenas curvo y no espiralado como en *Euophrys* o en ángulo como en *Phiale*. La apófisis de la tibia del palpo es gruesa, a veces tuberosa y no larga y delgada como en *Phiale* o bífida como en *Frigga* Koch 1846. Fémur y patela de pata III son más largos y gruesos que los de pata IV, mientras que tibia y metatarso III son más cortos o iguales a los de IV.

Descripción.—Ejemplares relativamente grandes: longitud total, machos 6.20–9.87, hembras 6.53–11.17. Prosoma con lados suavemente redondeados, ancho 74–93% del largo, alto 48–58% del largo. Área ocular ocupando 32–50% del largo del prosoma. Área ocular 52–58% más ancha que larga, tercera hilera ocular siempre más angosta que la primera. Altura del clípeo 30–40% del diámetro de OMA. OMP ligeramente más cerca de OLP que de OLA. Fórmula de patas: machos I-III-IV-II excepcionalmente III y IV iguales en longitud total; hembras IV-III-I-II, a veces III y IV subiguales. Quetotaxia: (variantes entre paréntesis). Machos: Fémures I d 1-1-1, p 2ap (r 1ap, p 1-2); II d 1-1-1, p 2ap, r 1-2 (r 1ap); III d 1-1-1, p 1-2 (p 2ap), r 1 (r 2, r 1-2); IV d 1-1-1, p 1ap (p 2ap), r 1ap. Patelas I, II p 1(r 1); III, IV p 1, r 1. Tibias I v 2-2-2, p 1-1 (p 1-1-1); II v 1r-2-2, p 1-1-1 (p 1-1); III, IV d 1b (d 1b-2ap, d 1b-1rap), v 1p-2, p 1-1-1, r 1-1-1. Hembras: I d 1-1-1, p 2ap (r 1ap); II d 1-1-1, p 2ap, r 1ap (r 1-1, r 1-2); III d 1-1-1, p 1-2 (p 2ap), r 1ap (r 2ap); IV d 1-1-1, r 1. Patelas II (p 1); III, IV p 1, r 1. Tibias I v 2-2-2, p 1-1 (p 1); II v 1r-2-2, p 1-1; III, IV v 1p-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v 2-2, p 1-2, r 1-1-2; IV v 2-2, p 1-1-2, r 1-1-2. La presencia de un par de espinas dorsales apicales además de la dorsal basal media en las tibias III y IV de los machos, no parece ser específica. A menudo estas espinas no son simétricas y en ejemplares del mismo lote pueden estar ausentes. Palpos: tibia con apófisis retrolateral o retrodorsal gruesa, tuberosa, a veces con una punta cónica dirigida basal, ventral o apicalmente (Figs. 3–13, 15, 16); cimbio con una depresión retrolateral basal de borde carenado, que puede faltar; bulbo con divisiones media y basal separadas por profundo surco (Figs. 14, 17, 19); división apical con émbolo cónico, recto o ligeramente curvo, acompañado por un conductor membranoso, casi paralelo, de base independiente (Figs. 19–31), [excepto en *F. maculatipes* (Cambridge 1901) Fig. 14]. Epigino (Figs. 36–43): placa circundada en el extremo anterior por un surco curvo de bordes ligeramente carenados; borde posterior con un bolsillo de copulación, a veces con bolsillos de anclaje laterales (Fig. 44); área media longitudinalmente algo elevada, en algunas especies claramente en forma de quilla (*F. regia,* Figs. 42, 43). Orificios de copulación en la mitad anterior de la placa, relativamente pequeños. Conductos de copulación en forma de embudo, espermatecas posteriores, ovoideas o esféricas (Figs. 44–57). La estructura interna de los conductos de copulación es compleja y no ha podido comprenderse, pese a intentar distintos tipos de clarificación (KOH, tripsina,
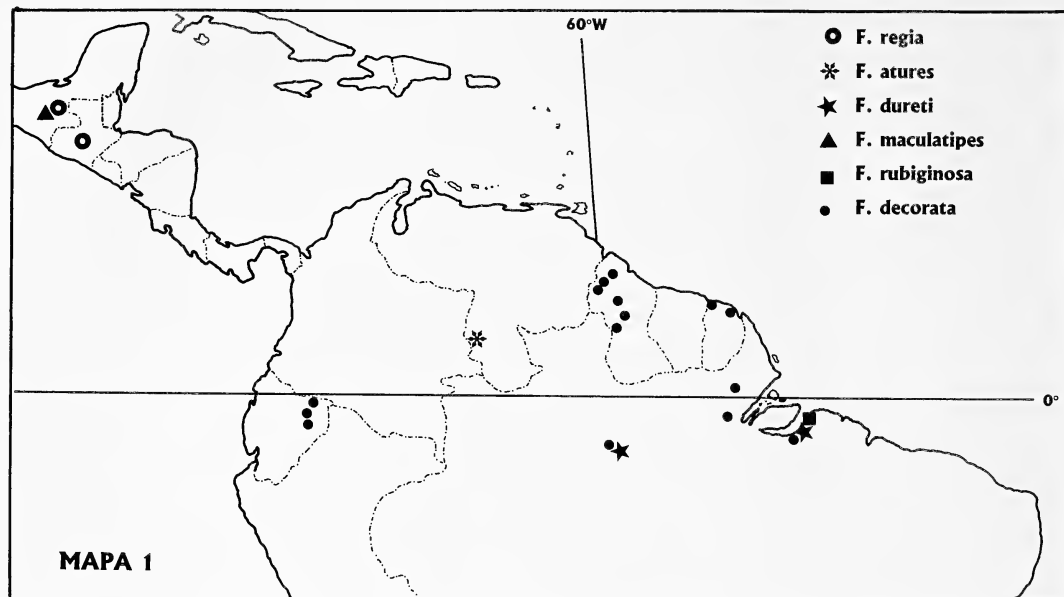
Mapa 1.—Distribución de las especies de *Freya* del grupo *decorata*. América Central, sur de México y norte de América del Sur.

prolasa). Parece posible que el conductor penetre en el conducto, ya que la distensión no lo separa del émbolo.

Freya decorata (C.L. Koch 1846)
Figs. 1–3, 12, 13, 19, 20, 27, 33, 36, 44, 49;
Mapa 1

Euophrys decorata C.L. Koch 1846: 200, fig. 1248 (macho de Brasil, Pará, no examinado).
Euophrys trifasciata C.L. Koch 1846: 201, fig. 1249. Simon 1903: 730.
Euophrys (Thore) trifasciata: C.L. Koch 1850: 66.
Euophrys (Freya) decorata: C.L. Koch 1850: 66.
Phyale decorata: C.L. Koch 1850: 59 (*sic*).
Atta (Freya) decorata: Simon 1864: 313.
Atta (Parthenia) trifasciata (Thore): Simon 1864: 313 (*sic*).
Freya regia: Simon 1903: 724, 730, fig. 858 (error de identificación).
Attus decoratus: Taczanowski 1871: 70.
Freya decorata: Simon 1903: 730, 739. Petrunkevitch 1911: 653. Caporiacco 1948: 717; 1954: 169, figs. 61, 61a–c. Roewer 1954: 1081. Bonnet 1956: 1919. Platnick 1997: 884.
Freya decorata var. *dyscrita* Penther 1900: 285, fig. 2. Petrunkevitch 1911: 653. Bonnet 1956: 1919.
Freya strandi Caporiacco 1947: 32; 1948: 717, fig. 148. [1 hembra, 2 machos y 1 hembra inmaduros, sintipos, en MLS, de British Guiana (Guyana), examinados]. Roewer 1954: 1083. NUEVA SINONIMIA.

Attus brandtii Taczanowski 1871: 72 (*Brandtii*) [3 machos de Guayana Francesa (uno de Cayena y dos de St. Laurent de Maroni) no examinados]. Petrunkevitch 1911: 596. Mello-Leitão 1948: 1920 (= *Freya brandti*). Bonnet 1955: 795. NUEVA SINONIMIA.

Descripción.—*Machos:* Longitud total 6.60–7.98 ($n = 20$, $\bar{x} = 7.30$). Ancho del prosoma 75–90% de su largo ($n = 21$, $\bar{x} = 80\%$); alto del prosoma 49–58% de su largo ($n = 9$, $\bar{x} = 53\%$); largo del área ocular 40–53% del largo del prosoma ($n = 14$, $\bar{x} = 44\%$); largo del área ocular 60–67% del mayor ancho del área ($n = 14$, $\bar{x} = 64\%$). Altura del clípeo 26–40% del diámetro de OMA ($n = 9$, $\bar{x} = 32\%$). Fórmula de patas: I-III-IV-II ($n = 7$), I-IV-III-II, IV y III subiguales ($n = 3$). Quetotaxia: como en el género. Palpos (Figs. 2, 3, 33): tibia maciza, con gran escotadura dorsal, cara retrolateral tuberosa, con borde superior recto, una apófisis triangular en el borde inferior de la cara interna, cuyo vértice se dirige hacia la base de la tibia. Esta apófisis es visible solamente en vista ventral o retroventral (Figs. 12, 13). Cimbio con una depresión transversa en retrodorsal basal, con borde superior ligeramente carenado. Embolo ligeramente curvo,

ancho en la base y agudo en el ápice; el conductor es una lámina membranosa, incolora, ligeramente plegada longitudinalmente y con el extremo libre curvado (Figs. 19, 20, 27), acompaña al émbolo en todo su trayecto y lo sobrepasa en el ápice. Color (Fig. 1): prosoma negro, con bandas y manchas de pelos blancos de la siguiente manera: anchas bandas submarginales que atrás terminan a cada lado del declive torácico y por delante continúan para formar la densa barba del clípeo; una gran mancha oval media en el margen anterior, que por detrás alcanza la altura del borde anterior de los OLP; desde el borde interno de cada OLA en margen anterior, una banda longitudinal hasta el borde anterior del OLP de su lado, a veces interrumpida en el medio; una mancha oval en la parte media de RC, delante de la estría, separada por algunos pelitos negros de la banda media torácica que se angosta hacia atrás y termina en la parte media del declive torácico. Opistosoma negro o pardo negruzco, con pelos al tono; una banda de tegumento amarillo cubierta por pelos blancos bordea la base y sigue por los lados, afinándose y terminando en el ápice o un poco antes; una banda media longitudinal de tegumento amarillo con pelos blancos desde la banda basal hasta el ápice; en algunos ejemplares separada de la basal por una zona con pelos negruzcos. Tubérculo anal blanquecino, con algunos pelitos blancos. Vientre pardo claro, con manchitas amarillas. Quelíceros pardo rojizo oscuro; láminas y labio pardos con bordes amarillentos. Pata I: fémur pardo oscuro, con la mitad dorsal basal pardo claro con escasos pelitos blancos; patella pardo oscuro, mitad dorsal basal amarillenta con pelos blancos y algunos pelos blancos en el borde distal; tibia y metatarso pardos, con el tercio medio amarillento con pelos blancos dorsales; tarso amarillo. Pata II: como I, pero pardo claro. Patas III y IV amarillentas. Palpos: fémur pardo negruzco, la mitad apical más clara, con largos pelos blancos dorsales y en el tercio apical una densa área de pelos blancos; patella con caras dorsal y prolateral con densos pelos blancos; tibia parda con pelos pardos; cimbio pardo, más claro hacia el ápice con pelos al tono.

Hembras: Longitud total 6.53–9.58 (n = 9, x̄ = 8.64). Ancho del prosoma 73–90% de su largo (n = 13, x̄ = 79%); alto del prosoma 48–55% de su largo (n = 8, x̄ = 51%); largo del área ocular 41–50% del largo del prosoma (n = 8, x̄ = 44%); largo del área ocular 61–66% del mayor ancho del área (n = 8, x̄ = 64%). Altura del clípeo 27–47% del diámetro de OMA (n = 8, x̄ = 33%). Fórmula de patas: IV-III-I-II (n = 5), III-IV-I-II (n = 1). Quetotaxia como en el género. Epigino (Figs. 36, 44, 49): placa limitada en su borde anterior por un surco curvo con bordes carenados; línea media longitudinal ligeramente elevada; orificios de copulación en el área anterior, ovales, con el eje mayor longitudinal. Borde posterior excavado, con bolsillos de anclaje laterales. Color: prosoma pardo rojizo oscuro con RC negruzca, cubierta por pelos escamosos semitransparentes, brillantes. En margen anterior, algunos escasos pelos blancos entre los OMA, entre OMA y OLA y entre OLA y OLP. RC limitada atrás por una banda pardo claro con forma de V invertida, con vértice en extremo posterior de la estría. En RT, a partir de la estría, dos bandas oscuras de cada lado, alternadas con bandas claras y una banda media longitudinal clara que llega al margen posterior. Sobre las bandas oscuras pelos traslúcidos como los de RC y sobre las claras, pelos blanquecinos, escasos. Clípeo con pelos largos amarillentos, que no forman barba. Opistosoma pardo claro, con pelos al tono. Bandas como en el macho, pero las laterales se interrumpen antes del tercio apical y son seguidas por una manchita alargada. La banda media se une a la basal o comienza en el tercio basal y continúa hasta el ápice. El borde interno de las bandas laterales y ambos bordes de la media, bordeados por bandas angostas pardo oscuro, con pelos al tono. Vientre pardo claro, la parte media con manchitas pardas. Pata I pardo claro, fémur, patella y tibia con tercio apical más oscuro, pelos blancos sobre las partes claras, metatarso y tarso amarillentos. Pata II: como I, pero más clara. Patas III y IV pardo amarillento, más oscuro en los ápices. Palpos: fémur amarillento, con pelos blancos dorsales; patella amarillenta con una mancha dorsal basal pardo oscuro y pelos blancos en la mitad distal; tibia y tarso pardo claro, con mancha oscura dorsal basal y pelos amarillos dorsales y laterales.

Material examinado.—BRASIL: *Pará:* Belém, 8 machos, 5 hembras, 5 inmaduros, N° 9654 MACN, agosto 1971 (Galiano); 1 macho, 2 hem-
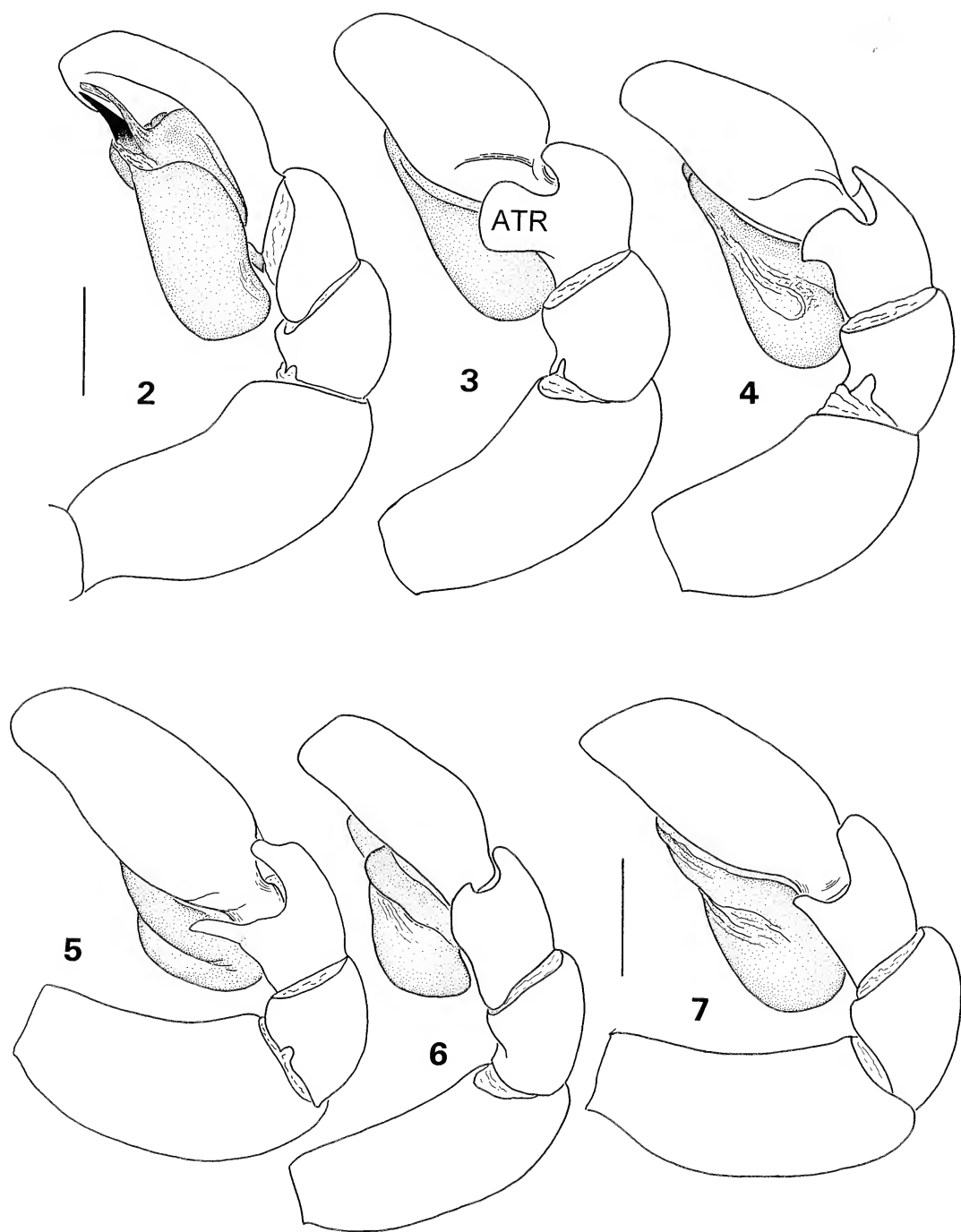
Figuras 2–7.—Palpos izquierdos. 2. *Freya decorata,* prolateral; 3. El mismo, retrolateral; 4. *F. chapare,* retrolateral; 5. *F. nigrotaeniata,* retrolateral; 6. *F. atures,* retrolateral; 7. *F. dureti,* retrolateral. Escalas = 0.5 mm.
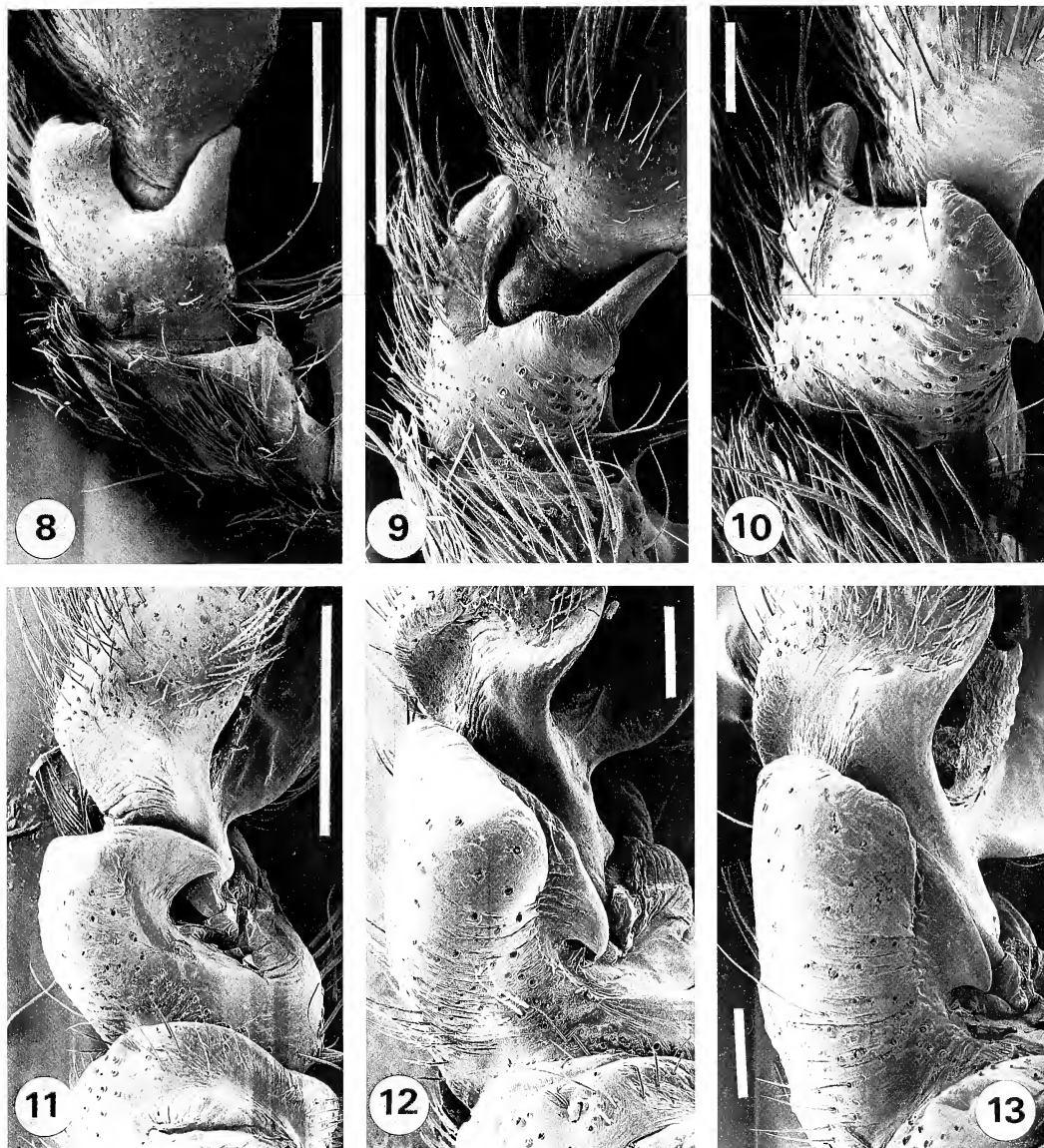
Figuras 8–13.—Tibias de palpos derechos, vista retrolateral. 8. *Freya dureti;* 9. *F. nigrotaeniata;* 10. *F. atures;* 11. *F. chapare;* 12. *F. decorata* de Guyana; 13. *F. decorata* de Pará. Escalas 8, 9, 11 = 0.5 mm; 10, 12, 13 = 100 μm.

bras, N° 9655 MACN, agosto 1970 (Galiano); 1 macho, N° 9656 MACN, marzo 1953 (Duret); 1 hembra (MPM) (Moenkhaus); 2 machos, (*F. regia* det. Simon) (MNHN); *Amapá:* Santana, río Matapí, 2 machos, N° 9657 MACN, junio 1966 (Galiano); Serra do Navio, 1 macho, 1 hembra, 1 inmaduro, N° 9658 MACN, junio 1966 (Galiano); *Amazonas:* Manaus, 1 hembra, N° 9690 MACN, agosto 1971 (Galiano). **GUYANA:** Upper Essequibo, Onoro Region, 1 macho, 1 hembra (MLS), 1–24 diciembre 1937 (Hassler). En MLS, colectado por Drs. Bec-

cari y Romiti, determinado por Caporiacco: Conwarook, Potaro, 2 machos, 1 hembra, 18 mayo 1936; Two Mouth, Essequibo, 1 macho, 14 julio 1936; Tumatumari, 3 machos, 19 setiembre 1936; Garroway Landing, Potaro, 1 macho inmaduro, 20 marzo 1936; Mackenzie, 1 hembra, setiembre 1931; Campo I, Demerara, Baboon Camp, 1 hembra, octubre 1931; Lungo il Cattle fra Campo V Curupucari, 1 macho, 8 noviembre 1931; Cannister Falls, Demerara, 1 macho, noviembre 1931. Uni-Con, 2 machos (MPM) (Parrish). **GUAYANA FRANCE-**

SA: S. Jean du Maroni, 2 hembras (MLS), 1914; Charvein, 1 macho (MLS), 1916. **ECUADOR:** *Napo:* Lago Agrio 270 m, 4 machos, Nº 9659 MACN, junio 1976 (Williner); Sacha 240 m, 1 macho, Nº 9660 MACN, junio 1976 (Williner); Limoncocha, 1 macho, 1 hembra, Nº 9661 MACN, abril 1984 (A. Roig).

Distribución.—Brasil: Estados de Pará, Amapá y Amazonas. Guyana. Guayana Francesa. Ecuador: Provincia de Napo.

Nota: Los caracteres de *Freya strandi* coinciden exactamente con los de las hembras de *Freya decorata* de Guyana y Guayana Francesa. El patrón de coloración así como la distribución de *Attus brandti* son iguales a los de *F. decorata,* por lo que se establece la simonimia. Los tipos de esta especie no son citados en el Catálogo de Prószyński (1971:380) por lo que es probable que estén perdidos.

Freya regia (Peckham & Peckham 1896)
Figs. 17, 18, 30, 31, 32, 42, 43, 46, 52;
Mapa 1

Heraclea regia Peckham & Peckham 1896: 77, pl. III, figs. 6, 6a-c, pl. IV, figs. 1, 1a-b (1 macho lectotipo, 1 hembra paralectotipo, 3 hembras, 3 machos paralectotipos, aquí designados, de Guatemala, Nº 807; 4 hembras, 1 macho inmaduro, sintipos, de Guatemala, Nº 789 en colección Peckham (MCZ), examinados).

Cyrene regia: Cambridge 1901: 222, 226, 229, pl. XVIII, figs. 12, 12a-g, 13, 13a-d.

Freya regia: Petrunkevitch 1911: 654. Caporiacco 1938: 279. Bonnet 1956: 1921. Roewer 1954: 1082.

Diagnosis.—Se diferencia de las otras especies de *Freya* del grupo *decorata* por presentar una saliente en ángulo recto en el borde interno del conductor, de modo que el tercio apical es más ancho que los dos tercios basales; por la apófisis triangular tibial retroventral más horizontal que en *F. decorata* y con el extremo romo; por carecer de manchas de pelos blancos en margen anterior del prosoma entre OMA y OLA. El epigino se distingue del de todas las otras especies del grupo por el borde posterior curvado hacia atrás y por una carena o quilla longitudinal media.

Descripción.—Lectotipo macho: Largo total 7.85. Prosoma largo 4.00, ancho 3.13, alto 1.87. Clípeo, alto 0.33. Área ocular largo 1.70, ancho de hilera anterior 2.70, de hilera posterior 2.47. Distancias OLA-OMP 0.47, OMP-OLP 0.33. Diámetro OMA 0.87. Fórmula de patas I-III-IV-II. Quetotaxia como en

el género, pero patella I sin espinas y tibia II p 1-1. Palpos (Figs. 17, 18, 32): cimbio sin la depresión retrodorsal basal presente en *F. decorata.* Conductor ligeramente más corto que el émbolo, laminar, de ápice redondeado, con un ensanchamiento en el tercio distal (Figs. 30, 31). Color: los sintipos están en regular estado de conservación y depilados en su mayor parte. Solamente algunos ejemplares conservan restos de pelos. Diferencias con *Freya decorata:* prosoma pardo oscuro con pelos negros, la RC con pelos rojizos; una mancha de pelos blancos en el margen anterior entre los OMA, una mancha oval de pelos blancos desde extremo anterior de la estría torácica hasta el declive torácico, donde se bifurca y se une a las bandas laterales. Opistosoma pardo, cubierto por pelos rojo pardusco.

Paralectotipo hembra: Largo total 10.37. Prosoma largo 4.27, ancho 3.53, alto 2.27. Clípeo, alto 0.33. Área ocular largo 1.87, ancho de hilera anterior 2.87, de hilera posterior 2.73. Distancias OLA-OMP 0.50, OMP-OLP 0.33. Diámetro OMA 0.93. Fórmula de patas IV-III-I-II. Quetotaxia como en el género. Epigino (Figs. 42, 43, 46, 52): borde posterior curvado hacia atrás; una carena media longitudinal separa dos depresiones en las que se abren los orificios de copulación circulares. Color: como en *F. decorata,* excepto: prosoma pardo rojizo, con escasos pelos blancos laterales. Opistosoma pardo, con pelos rojos; una banda media longitudinal desde la parte media hasta cerca del ápice, de pelos blanco amarillento; una banda de pelos blanco amarillento circunda la base y se continúa por los lados hasta aproximadamente el medio, seguida por dos manchas de cada lado, la apical más alargada. Patas pardas, todos los fémures, patellas y tibias II a IV con el tercio medio amarillo con pelos blancos. Palpos: fémur pardo claro con manchita apical amarilla con pelos blancos; patella y tibia pardo oscuro con tercio apical amarillo con pelos blancos.

Material examinado.—Sólo la serie de sintipos.

Distribución.—Guatemala; México: Chiapas.

Nota: Para colorido, ver Peckham y Peckham (1896) y Cambridge (1901).
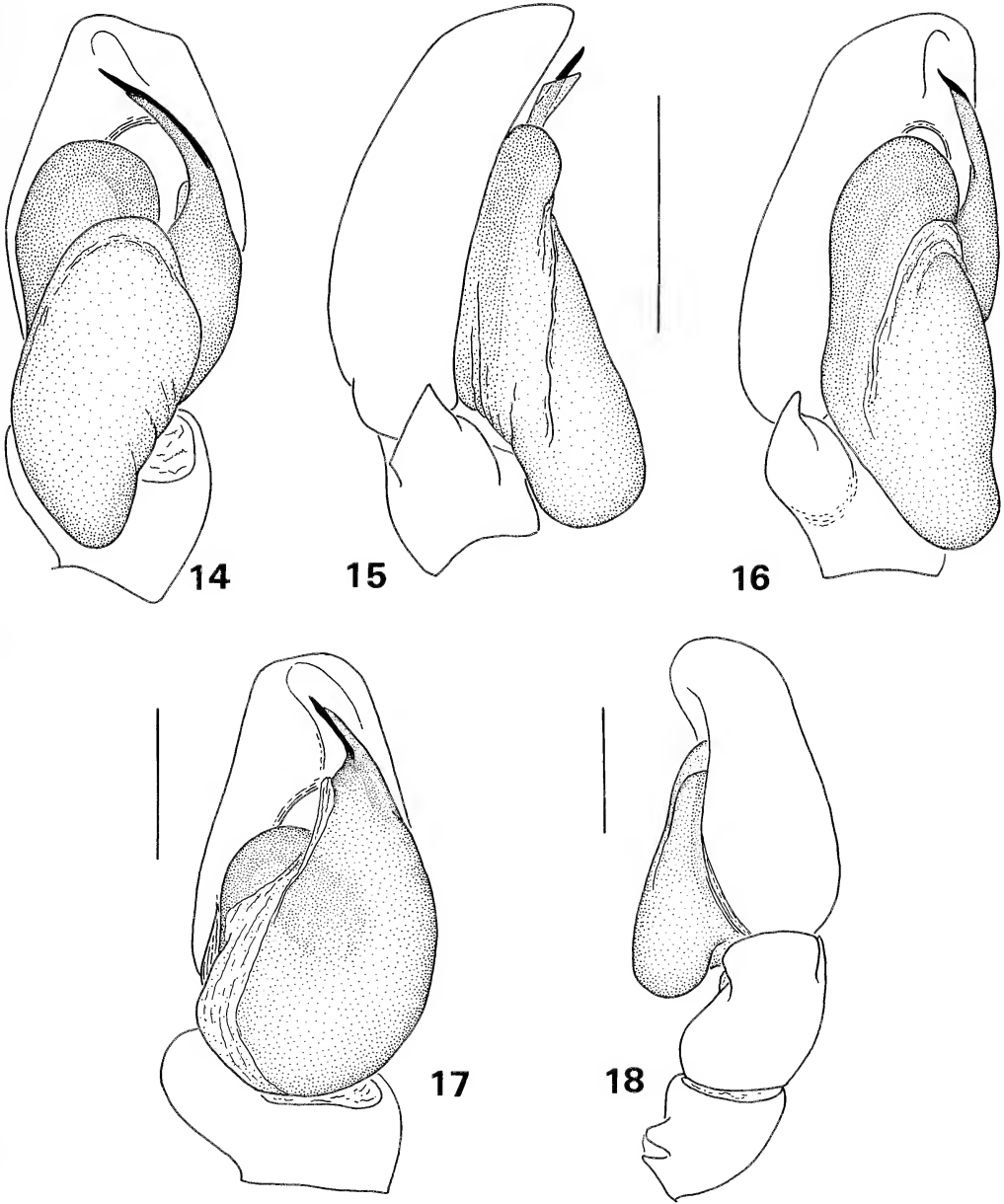
Figuras 14–18.—14–16. *Freya maculatipes.* 14. Palpo derecho, ventral; 15. El mismo, retrolateral; 16. El mismo, retroventral. 17. *F. regia,* palpo derecho, ventral; 18. *F. regia,* palpo izquierdo, retrolateral. Escalas = 0.5 mm.

Los especímenes machos procedentes de Brasil, Pará, que E. Simon (1903: 724, 730, fig. 858) determinó como *F. regia,* son en realidad *F. decorata* y las hembras tienen epigino similar a *Freya rubiginosa.* Este error de identificación no altera los caracteres diagnósticos que Simon dio para el género (Simon 1903: 739).

Freya rubiginosa (C.L. Koch 1846) nueva combinación
Figs. 38, 45, 50; Mapa 1

Euophrys rubiginosa C.L. Koch 1846: 209, fig. 1255 (hembra holotipo, N° 1803 en ZMB, de Brasil, Pará, examinado). Petrunkevitch 1911: 649. Bonnet 1956: 1887; 1959: 4697. Roewer 1954: 1181.
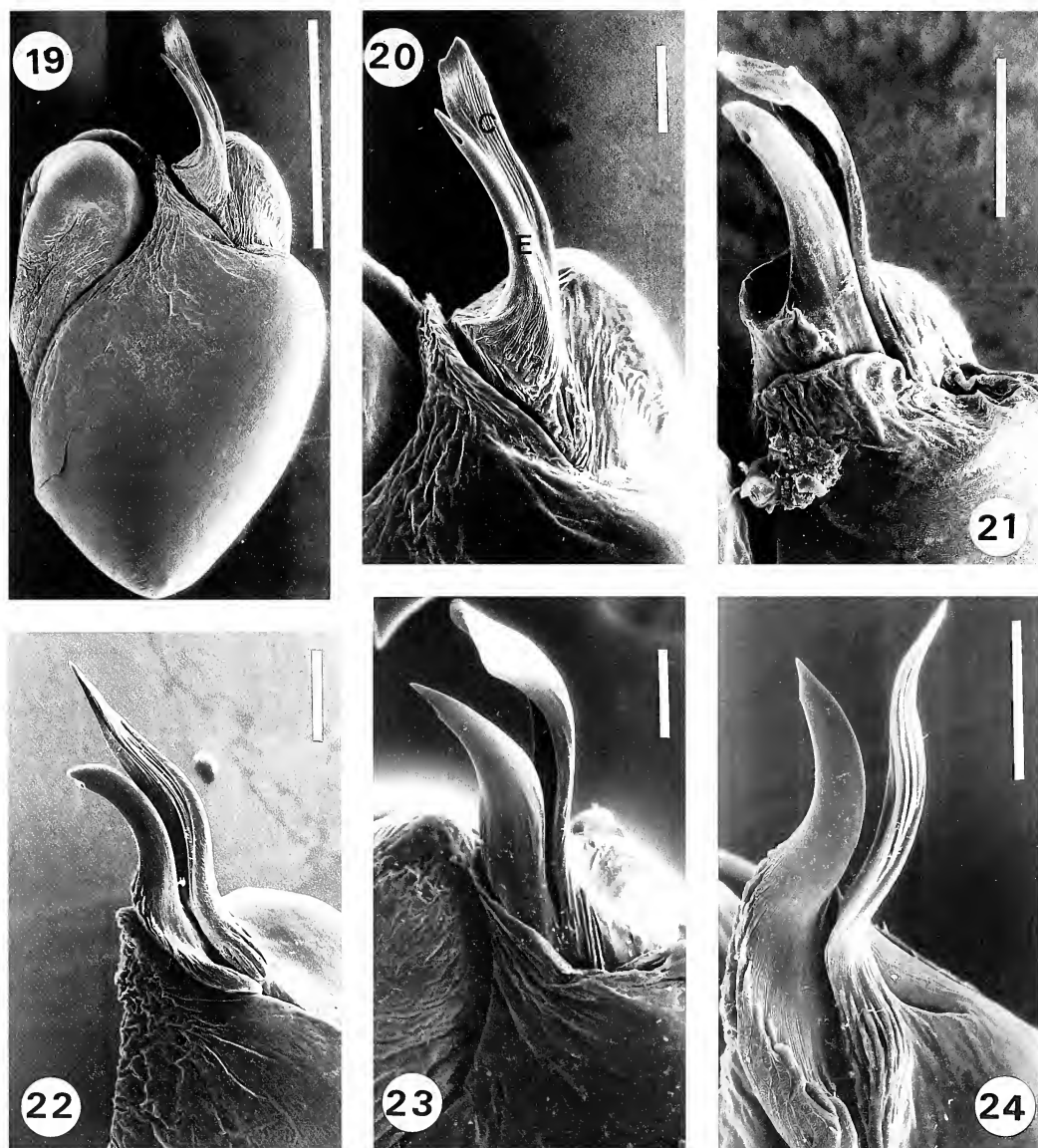
Figuras 19–24.—19. Bulbo, vista ventral. 20–24, Embolos y conductores. 19, 20. *Freya decorata;* 21. *F. atures;* 22. *F. chapare;* 23. *F. dureti;* 24. *F. nigrotaeniata.* Escalas 19 = 0.5 mm, 20–24 = 100 μm.

Euophrys (*Trivia*) *rubiginosa:* C.L. Koch 1850: 68.
Atta (*Trivia*) *rubiginosa:* Simon 1864: 314.

Diagnosis.—Se diferencia de las otras especies del grupo por tener el borde posterior del epigino con una escotadura apenas excavada.

Descripción.—Holotipo hembra: Clípeo, alto 0.27. Área ocular largo 1.73, ancho de hilera anterior 2.73, de hilera posterior 2.60. Distancia OMA-OLA 0.40, OMP-OLP 0.40. Diámetro OMA 0.93. Epigino: Fig. 38.

Hembra: (Nº 9663 MACN comparada con el holotipo). Largo total 9.66. Prosoma largo 4.33, ancho 3.33, alto 2.00. Clípeo, alto 0.23. Área ocular largo 1.77; ancho de hilera anterior 2.83, de hilera posterior 2.73. Distancias OLA-OMP 0.50, OMP-OLP 0.43. Diámetro OMA 0.90. Fórmula de patas III-IV-I-II. Quetotaxia como en el género. Opistosoma largo 5.33. Epigino (Figs. 45, 50): borde posterior con una leve escotadura. Borde anterior con surco profundo, curvo, de bordes carenados. Orificios de copulación circulares o apenas alargados transversalmente. Conductos de co-

Figuras 32–35.—Tibias del palpo derecho, vista dorsal. 32. *Freya regia;* 33. *F. decorata;* 34. *F. atures;* 35. *F. chapare.* Escalas = 0.5 mm.

Figuras 25–31.—Palpos: Embolos y conductores. 25. *Freya atures,* dorsal; 26. Los mismos, proventral; 27. *F. decorata,* ventral; 28. *F. dureti,* ventral; 29. Los mismos, prolateral; 30. *F. regia,* retrolateral; 31. Los mismos, ventral. Escalas = 100 μm.

pulación muy anchos, tocándose en la línea media o apenas separados. Espermatecas pequeñas, esféricas. Color: como en *F. decorata,* con estas diferencias: prosoma pardo, con la RC más oscura, cubierta por pelos pardo rojizo, transparentes, brillantes; algunos pelos blanco amarillento en margen anterior, entre los OMA y entre OMA-OLA; una mancha triangular de esos pelos delante de la estría torácica. Desde extremo anterior de la estría hasta margen posterior de RT, una banda media longitudinal amarilla con pelos blancos.

Opistosoma pardo, las áreas entre las bandas blancas con pelos pardos con reflejos rojizos.

Variantes.—En una de las hembras las bandas laterales del opistosoma se interrumpen en la mitad y se continúan con dos manchas alargadas.

Nota.—El holotipo estaba pinchado en alfiler, según el uso de la época. Con autorización del Dr. Moritz, se procedió a ablandarlo, retirarle el alfiler y se disecó el epigino que se ilustra (Fig. 38).

Material examinado.—BRASIL: *Pará:* Belém, 1 hembra, N° 9663, MACN, comparada con el tipo, agosto 1970 (Galiano); 2 hembras, N° 9662 MACN, agosto 1971 (Galiano); 1 hembra determinada como *Freya regia,* probablemente por Simon (MNHN).

Distribución.—Sólo de la localidad tipo.

Freya nigrotaeniata (Mello-Leitão 1945)
nueva combinación
Figs. 5, 9, 24, 37, 56, 57; Mapa 2

Phiale nigrotaeniata Mello-Leitão 1945: 292, fig. 82 (1 hembra y 1 macho sintipos, inmaduros, N° 16.825 en MLP, de Argentina, Corrientes, Goya, examinados). Roewer 1954: 1062. Galiano 1981: 13 (sp. inq.)

Freya regia: Mello-Leitão 1941: 203 (identificación errónea); 1942: 383 (identificación errónea).
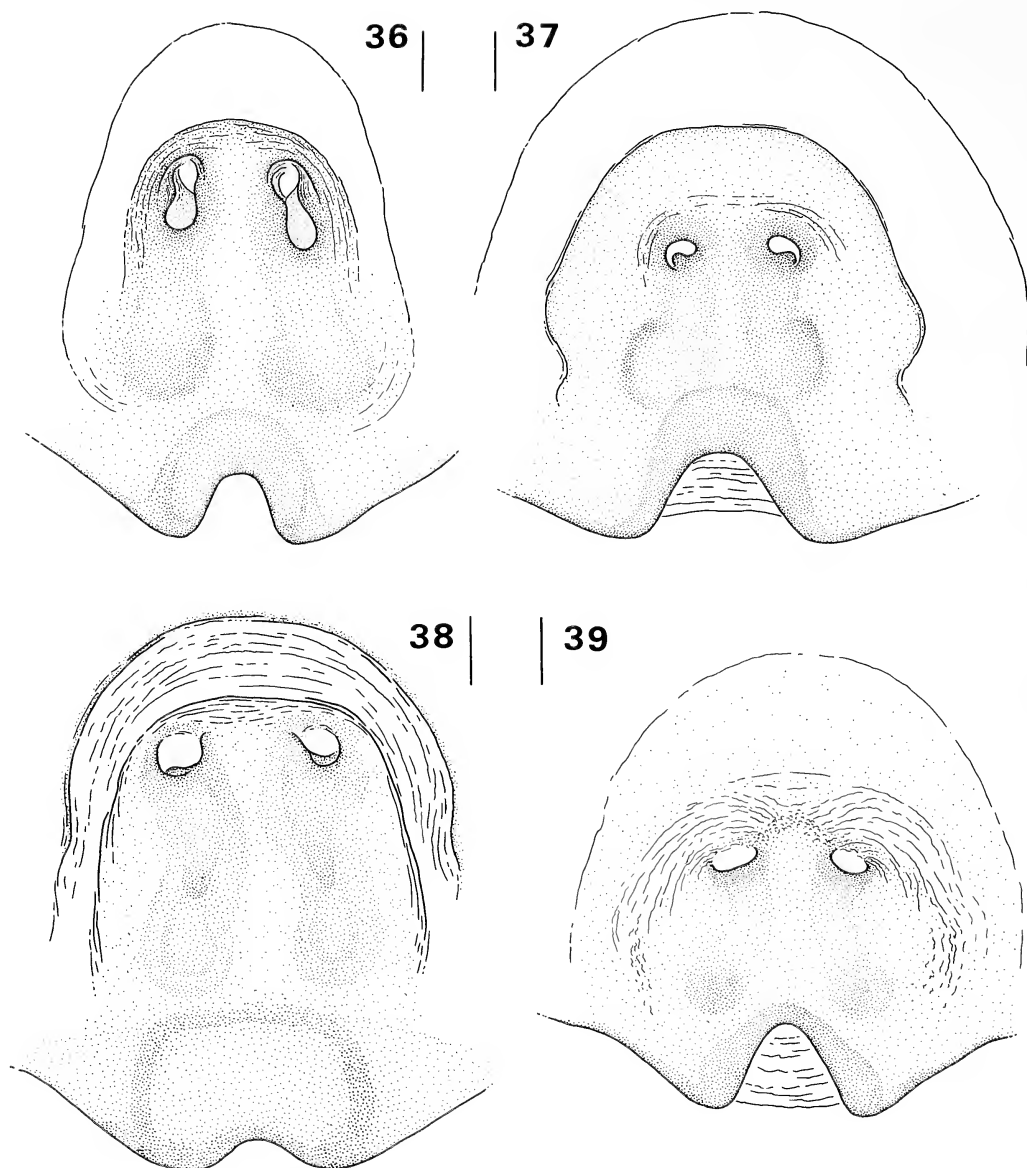
Figuras 36–39.—Epiginos, vista ventral. 36. *Freya decorata;* 37. *F. nigrotaeniata;* 38. *F. rubiginosa;* 39. *F. atures.* Escalas = 100μm.

Diagnosis.—Se diferencia de *F. decorata* por tener en el palpo dos apófisis tibiales cónicas: una retrodorsal, corta y de ápice romo y otra retroventral, larga, de ápice agudo y granulada en la base, dirigida hacia el ápice. El conductor es más largo que el émbolo, ancho en la base y agudo hacia el ápice. El epigino se diferencia del de *F. decorata* por tener una gran escotadura en margen posterior, los orificios de copulación circulares y los conductos de copulación más cortos.

Descripción.—*Machos:* Longitud total 6.67–9.31 ($n = 9$, $\bar{x} = 8.26$). Macho Nº 9666 MACN: Longitud total 9.31. Prosoma largo 4.20, ancho 3.27, alto 2.00. Clípeo, alto 0.27. Área ocular largo 1.60, ancho de hilera anterior 2.60, de hilera posterior 2.47. Distancias OL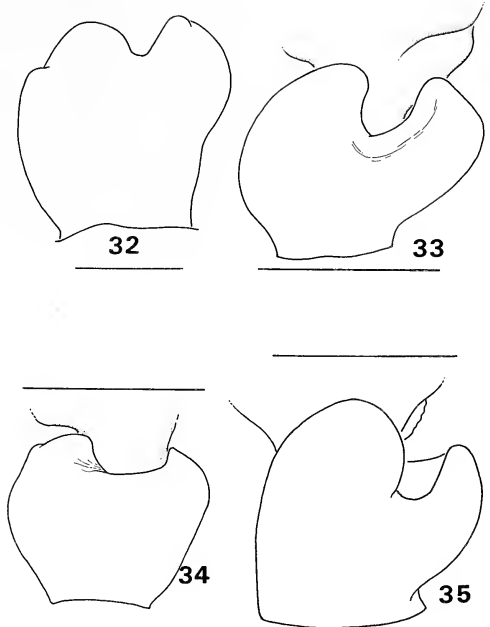A-OMP 0.43, OMP-OLP 0.40. Diámetro OMA 0.80. Palpos (Figs. 5, 9, 24): cimbio sin depresión retrodorsal basal. Fórmula de patas y quetotaxia como en el género. Color "in vivo": prosoma negruzco, con pelos negros;

banda marginal de pelos negros; anchas bandas laterales submarginales de pelos blancos, desde cada lado del declive torácico hacia adelante, donde forman la barba del clípeo, recta bajo los ojos anteriores, espacio entre los OMA ocupado por pelos negros; banda media longitudinal de pelos blancos desde margen anterior de RC hasta la mitad del declive torácico, donde se bifurca y se une a las bandas blancas laterales. En cada lado de RC, una bandita de pelos blancos desde margen anterior, mitad externa de OLA, hasta borde anterior de OLP. Tanto estas bandas como la media en la RC, están bordeadas por pelos rojos. Quelíceros negros con largos pelos blancos cerca de la base de cara anterior. Piezas labiales pardo oscuro con bordes amarillos; esternón pardo claro con margen oscuro. Opistosoma negro, con banda basal transversa de pelos blancos que se continúa por los lados hasta el tercio apical, ensanchándose levemente en el último tramo; banda media longitudinal de pelos blancos unida a la basal y terminando en el ápice. Tanto esta banda como las laterales, bordeadas por pelos rojos. El espacio entre la banda media y las laterales con pelos negros y rojo apagado mezclados, estos últimos más densos en el área central de cada lado. Tubérculo anal amarillo, con pelos blancos. Pata I pardo rojizo, fémur negruzco en el tercio apical, con algunos pelos blancos en dorso apical; patella con ápice negruzco y pelos blancos en parte media dorsal y prolateral apical; tibia pardo oscuro en los tercios basal y apical, tercio medio pardo claro con pelos blancos; metatarso pardo claro con tercio apical negruzco y escasos pelos blancos en el tercio basal dorsal. Pata II como I pero más clara. Patas III y IV pardo amarillento, algo más oscuras en ápices de fémures, tibias y metatarsos. Palpos pardo muy oscuro, con densísimos y largos pelos blancos en dorso apical de fémur y dorso de patella.

Hembras: Largo total 8.11–11.17 (n = 12, $\bar{x}$ = 10.00). Hembra N° 9665 MACN: Largo total 10.91. Prosoma largo 4.40, ancho 3.47, alto 2.07. Clípeo, alto 0.27. Área ocular largo 1.73, ancho de hilera anterior 2.83, de hilera posterior 2.77. Distancias OLA-OMP 0.40, OMP-OLP 0.40. Diámetro OMA 0.90. Fórmula de patas y quetotaxia como en el género. Opistosoma largo 6.33. Epigino (Figs. 37, 56, 57). Color "in vivo": prosoma pardo negruzco, con RC negra; RT con cuatro o cinco bandas radiantes pardo claro; sobre RC pelos negros y rojo bronceado mezclados, brillantes y traslúcidos. Sobre las bandas claras de RT pelos blancos, brillantes, poco densos; sobre las bandas oscuras pelos como en RC. Pelos blancos en margen anterior, escasos entre OMA y entre OMA y OLA, formando una manchita delante de la estría y una banda poco densa desde la estría hasta mitad del declive torácico. Clípeo sin barba, con largos pelos blancos en el margen. Opistosoma pardo; banda basal transversa amarillenta con pelos blancos, bandas laterales se adelgazan dos veces antes de llegar al ápice; banda media longitudinal amarilla con pelos blancos, desde la basal hasta el ápice. Estas bandas están bordeadas por pelos negros; la parte del dorso entre la banda media y las laterales con tegumento pardo y pelos rojo apagado, sin brillo. Vientre con manchitas pardas. Pata I: fémur con mitad basal amarilla y apical pardo oscuro; patella y tibia pardas con mancha media amarilla con pelos blancos; metatarso pardo claro con extremo apical oscuro. Pata II como I. Patas III y IV pardo claro, todos los artejos oscurecidos en ambos extremos. Palpos: fémur, patella y tibia amarillos con mancha basal dorsal pardo oscuro; tarso pardo con mancha dorsal basal negruzca.

Material examinado.—En MACN; **ARGENTINA:** *Santa Fe:* Las Gamas, 20 km de Vera, 1 hembra, N° 9665, 27–30 octubre 1994 (Ramírez & Faivovich); 1 macho, N° 9666; 4 hembras, 2 machos y 7 inmaduros, N° 9664, todos descendientes de la hembra N° 9665; *Salta:* Quebrada de Piquirenda, 1 macho, N° 9667, octubre 1966 (Hepper); Aguas Blancas, 2 machos, 1 inmaduro, N° 9668, abril 1984 (E. Maury); 1 macho, 6 inmaduros, N° 9669; marzo 1967 (Galiano); Finca Jakulica 25 km NO de Aguas Blancas, 1 macho, N° 9679, noviembre 1994 (Goloboff & Ramírez); El Tabacal, 1 macho, N° 9671, junio-julio 1933 (Daguerre); Urundel, 1 macho, 1 hembra, N° 9672, diciembre 1954 (Birabén); La Quena, río Bermejo, 1 hembra, N° 9673, mayo 1983 (Goloboff). *Jujuy:* El Cafetal, 1 macho, N° 9674, julio 1978 (Williner); Yuto, El Pantanoso, 1 hembra, N° 9675, noviembre 1966 (Galiano). *Chaco:* Selva del Río de Oro, 2 hembras, N° 9676, enero 1965 (Galiano); Resistencia, 1 hembra, 2 inmaduros, N° 9677, junio-julio 1977 (Carbajal). *Corrientes:* Santiago Alcorta, 2 hembras, N° 9678, junio 1943 (Biraben); Ituzaingó, 1 hembra, N° 9679, noviembre 1963 (Partridge). **PARAGUAY:** *Dpto. Presidente Hayes:* Ruta Transchaco km 193, 1 hembra, N° 9680, julio 1990 (Ramírez).

Distribución.—Argentina: Corrientes, Santa Fe, Salta, Jujuy, Chaco. Paraguay: Depto. Presidente Hayes.

Nota.—La hembra Nº 9665 fue mantenida en el laboratorio donde efectuó un desove, se crió la descendencia y obtuvieron adultos, entre ellos el macho Nº 9666. La observación de los juveniles durante su desarrollo permitió identificarlos con los tipos inmaduros de la especie.

Freya maculatipes (F.O.P.-Cambridge 1901)
Figs. 14-16; Mapa 1

Cyrene maculatipes Cambridge 1901: 225, 234, pl. XIX fig. 12, 12a-d (macho holotipo de México, Chiapas, Teapa, 1905–210 en NHM, examinado).
Freya maculaticeps: Simon 1903: 730 (lapsus).
Freya maculatipes: Petrunkevitch 1911: 654. Roewer 1954: 1082. Bonnet 1956: 1920.

Diagnosis.—Esta especie se diferencia de todas las otras del grupo *decorata* porque el émbolo y el conductor tienen una base común y se separan aproximadamente en la mitad de su trayecto.

Descripción.—*Macho holotipo:* Área ocular largo 1.33, ancho de hilera anterior 2.03, de hilera posterior 2.00. Distancias OLA-OMP 0.33, OMP-OLP 0.30. Fórmula de patas I-III-IV-II. Quetotaxia como en el género, salvo que metatarsos I y II tienen 1 prolateral apical. Palpos (Figs. 14–16): apófisis tibial gruesa, con punta aguda dirigida hacia el cimbio. Cimbio sin depresión retrodorsal basal. Embolo y conductor con origen común, el conductor más corto que el émbolo y con el extremo apical truncado. Color: ver descripción original. Aparentemente coincide con el de las especies del grupo *decorata,* excepto por los pelos anaranjados brillantes en RC y en los fémures, y por la banda media dorsal del opistosoma, que en su mitad distal está formada por chevrons unidos por los vértices.

Distribución.—Sólo la localidad tipo.

Nota.—Único ejemplar de la especie conocido, está atravesado por un alfiler entomológico que penetra por el esternón, sale por el declive torácico, entra en el opistosoma por el pedicelo y sale por la parte ventral delante de las hileras. No se pueden realizar otras medidas que las del área ocular. Es con ciertas dudas que se incluye esta especie en el grupo. Pese a que Cambridge (1901) señala que es muy similar a *Cyrene curvispina* Cambridge 1901, no es así, puesto que esta última especie

[actualmente un sinónimo de Nycerella sanguinea (Peckham & Peckham 1896) Galiano 1982] carece de conductor. Tal vez el hallazgo de las hembras de la especie permita una definición en cuanto a su correcta ubicación.

Freya dureti nueva especie
Figs. 7, 8, 23, 28, 29, 41, 48, 51; Mapa 1

Tipos.—Macho holotipo, Nº 9681 MACN de Brasil, Pará, Belém, (elev. 11 m; 01°28'S, 48°29'W) agosto de 1953 (P. Duret); 1 macho paratipo en MNRJ, de Brasil, Amazonas, Manaus (elev. 93 m; 03°08'S, 60°02'W) Reserva Ducke (26 km desde Manaus), agosto 1971 (Galiano); 1 hembra alotipo, Nº 9682 MACN, de igual localidad y colector.

Etimología.—La especie se nombra en honor del entomólogo Dr. José Pedro Duret, quien coleccionó abundantes arañas durante sus viajes de estudio.

Diagnosis.—Se diferencia de *F. decorata* y de *F. nigrotaeniata* por tener el prosoma más robusto y por carecer de manchas o bandas de pelos blancos en el margen anterior de la RC. De *F. decorata* se distingue además por tener la apófisis tibial palpal retrolateral cónica. El conductor, con el extremo distal redondeado, a diferencia de *F. nigrotaeniata* donde dicho extremo es agudo.

Descripción.—*Holotipo macho:* Largo total 9.86. Prosoma largo 4.67, ancho 4.00, alto 2.40. Clípeo, alto 0.33. Área ocular largo 1.97, ancho de hilera anterior 2.83, de hilera posterior 2.70. Distancias OLA-OMP 0.50, OMP-OLP 0.43. Diámetro OMA 0.93. Palpos (Figs. 7, 8, 23, 28, 29): el cimbio carece de la depresión retrodorsal basal de *F. decorata.* La apófisis tibial es cónica, pero no tiene la base ensanchada y granulada presente en *F. nigrotaeniata.* Fórmula de patas I-IV-III-II, IV y III subiguales. Quetotaxia como en el género. Opistosoma, largo 5.20. Color: prosoma pardo negruzco con RC negra, pelos pardo negruzco, con algunos reflejos rojizos; no existen tres manchas ni banda transversa de pelos blancos en el margen anterior; banda longitudinal media de pelos blancos que comienza en mitad de la RC, pasa sobre la estría y se amplía formando un rombo en RT, terminando al comienzo del declive torácico; bandas laterales de pelos blancos casi marginales, muy anchas, bien separadas en el declive de RT, se continúan hacia adelante pero no ocupan todo
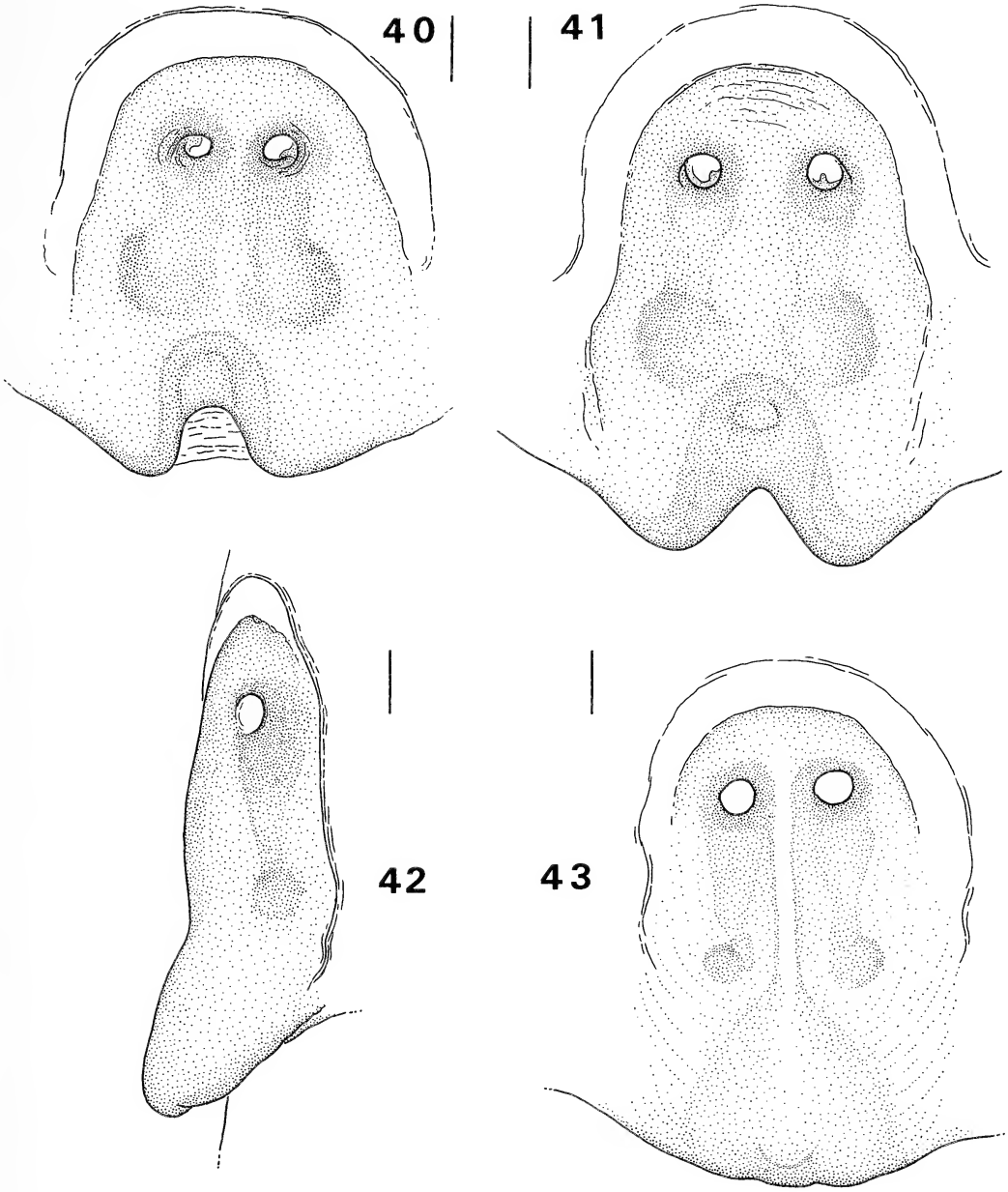
Figuras 40–43.—Epiginos. 40. *Freya chapare;* ventral. 41. *F. dureti,* ventral; 42. *F. regia,* lateral; 43. El mismo, ventral. Escalas = 100 μm.

el espacio bajo los ojos laterales y en el clípeo forman la barba, de borde superior recto, que deja libre un espacio bajo los cuatro ojos anteriores. Quelíceros pardo oscuro; piezas labiales pardo rojizo, con márgenes más claros. Esternón pardo rojizo. Opistosoma pardo oscuro con manchitas amarillas, cubierto por pelos pardos con reflejos rojizos; angosta banda basal de pelos blancos, que se continúa por los lados y se angosta en la parte media, terminando antes del ápice; banda media dorsal longitudinal de pelos blancos desde el tercio basal hasta cerca del ápice. Tubérculo anal amarillo con escasos pelitos blancos. Vientre pardo, con ancha banda media negruzca. Patas pardo rojizo oscuro con las siguientes áreas pardo amarillento: pata I con banda basal en patella y mancha media dorsal en tibia con
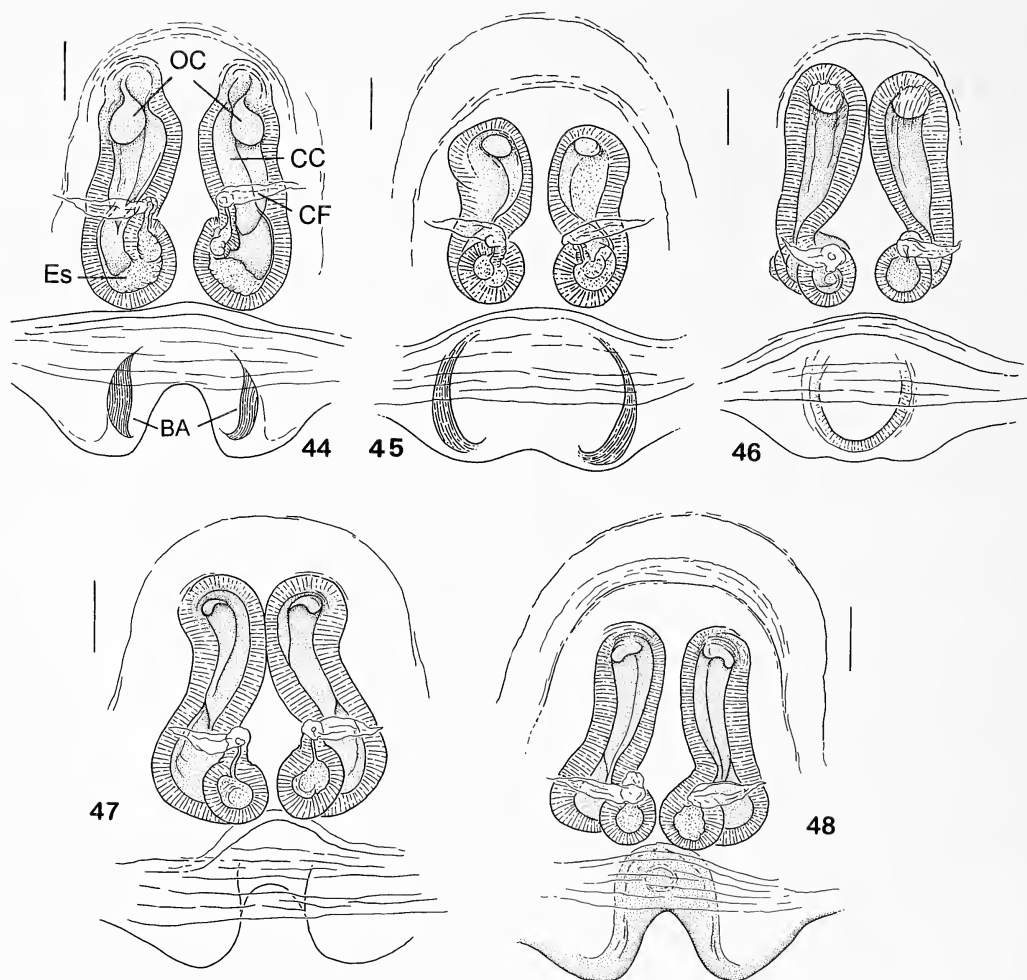
Figuras 44–48.—Epiginos clarificados, vista dorsal. 44. *F. decorata;* 45. *F. rubiginosa;* 46. *F. regia;* 47. *F. chapare;* 48. *F. dureti.* Escalas = 100 μm.

pelos blancos, metatarso en los dos tercios basales, todo el tarso. Patas II, III y IV, fémures con mancha media dorsal, mitad basal de patellas y mancha media dorsal de tibias, todas con pelos blancos; metatarsos pardos, con ápices negruzcos; tarsos pardo claro. Palpos como en el género.

Alotipo hembra: Largo total 8.11. Prosoma largo 3.87, ancho 2.93, alto 1.87. Clípeo, alto 0.23. Área ocular largo 1.53, ancho de hilera anterior 2.50, de hilera posterior 2.40. Distancias OLA-OMP 0.40, OMP-OLP 0.37. Diámetro OMA 0.77. Fórmula de patas y quetotaxia como en el género. Epigino: Figs. 41, 48, 51. Color: como en *F. decorata,* sin banda media longitudinal de pelos blancos en RT; la banda media longitudinal del opistosoma se-

parada de la basal; cada banda lateral llega hasta el tercio apical y es seguida por una mancha de pelos blancos, que no alcanza el ápice. Patas amarillas, la I con una mancha retrolateral basal y el tercio apical del fémur pardo oscuro; patella y tibia pardas con tercio medio amarillo. Palpos amarillos; patella, tibia y tarso con mancha dorsal basal pardo oscuro.

Distribución.—Brasil: Estados de Amazonas y Pará.

Nota.—Los dos ejemplares machos estudiados provienen de localidades alejadas pero son sin duda de la misma especie. Como se ha visto en el caso de *F. decorata,* la distribución desde el Alto Amazonas hasta su desembocadura se observa también en esa y otras especies. En Manaus se han coleccio-

nado ejemplares femeninos que pertenecen a dos especies diferentes: una hembra que se determina como *F. decorata* y otra que aquí se describe como la hembra de *F. dureti*. En Pará se encuentran *F. decorata, F. rubiginosa* y *F. dureti*. Existe la posibilidad de que *F. rubiginosa* sea la hembra de *F. dureti*. No puede tenerse en este grupo la certeza de la coespecificidad de ejemplares de distinto sexo, por lo que se mantiene el status de *F. rubiginosa*.

Freya chapare nueva especie
Figs. 4, 11, 22, 35, 40, 47, 53; Mapa 2

Tipos.—Holotipo macho, N° 9683 MACN y 2 machos paratipos, N° 9684 MACN, de Bolivia, Cochabamba, Depto. Chapare, Cristalmayo, febrero 1971 (A. Martínez); 5 machos paratipos, N° 9685 MACN, y 1 hembra Alotipo, N° 9686 MACN, de Bolivia, Chapare, Chimoré (coordenadas aproximadas 17°S, 66°W), enero 1972 (M. Fritz).

Etimología.—El nombre de la especie deriva de la localidad tipo.

Diagnosis.—Se diferencia de *F. decorata* por la forma de la apófisis tibial retrolateral, que es menos voluminosa y con la punta triangular anterior dirigida hacia la cara ventral de la tibia y no hacia la base, como en *F. decorata*. Se distingue de *F. nigrotaeniata*, cuyo émbolo y conductor son semejantes, porque en esta última especie la apófisis tibial es cónica. El epigino es muy semejante al de *F. nigrotaeniata*, del cual se diferencia apenas por tener los conductos de copulación algo más largos.

Descripción.—*Holotipo macho:* Largo total 7.71. Prosoma largo 3.93, ancho 2.90, alto 1.87. Clípeo, alto 0.27. Área ocular largo 1.43, ancho de hilera anterior 2.43, de hilera posterior 2.35. Distancias OLA-OMP 0.40, OMP-OLP 0.37. Diámetro OMA 0.80. Fórmula de patas y quetotaxia como en el género. Palpos (Figs. 4, 11, 22, 35): cimbio con depresión retrodorsal poco profunda. Apófisis retrolateral con borde superior recto, separada de la dorsal por una profunda escotadura. Extremo anterosuperior con una punta aguda, dirigida hacia cara ventral del palpo. Conductor membranoso, ligeramente plegado longitudinalmente, más largo que el émbolo y terminado en una punta aguda. Color: como en *F. decorata*, con estas diferencias: la banda longitudinal media de pelos blancos de RT se bifurca en el declive torácico y cada rama se une con pocos pelos a las bandas submarginales. La banda longitudinal media de pelos blancos del dorso del opistosoma, se une a la basal y termina en el ápice, así como las laterales. El dorso entre estas bandas tiene pelos pardo negruzco, con reflejos rojizos.

Alotipo hembra: Largo total 8.11. Prosoma largo 3.67, ancho 3.40, alto 1.80. Clípeo, alto 0.23. Área ocular largo 1.43, ancho de hilera anterior 2.40, de hilera posterior 2.36. Distancias OLA-OMP 0.40, OMP-OLP 0.33. Diámetro de OMA 0.73. Fórmula de patas y quetotaxia como en el género. Epigino: Figs. 40, 47, 53. Color: como en *F. decorata*, con las bandas radiantes torácicas bien evidentes pero sin banda longitudinal media de pelos blancos en RT.

Material estudiado.—**BRASIL:** *Goiaz:* Faz. Aceiro Yatai, 1 macho, octubre 1962 (Exp. Depto. Zoología) (MZSP).

Distribución.—Bolivia: Cochabamba. Brasil: Goiaz.

Nota:—Tres de los machos paratipos presentan d 1b-2ap espinas en tibias III y IV.

Freya atures nueva especie
Figs. 6, 10, 21, 25, 26, 34, 39, 54, 55; Mapa 1

Tipos.—Macho holotipo, N° 9687 MACN, 1 hembra alotipo, N° 9688 MACN, 2 hembras paratipos, N° 9689 MACN, de Venezuela, Territorio Federal de Amazonas, Atures (confluencia de los ríos Alto Orinoco y Cataniapo), junio 1976 (A. Martínez).

Etimología.—El nombre de la especie deriva de la localidad tipo.

Diagnosis.—Se diferencia de *F. decorata* porque en lugar de tres manchas de pelos blancos en margen anterior de RC tiene una banda transversa de pelos blancos desde el borde interno de un OLA al del otro; el cimbio carece de depresión retrodorsal basal; la apófisis tibial retrolateral tiene una prolongación cónica dorsal, el borde superior oblicuo y la punta anterior está dirigida hacia la base de la tibia; émbolo con una envoltura basal membranosa, que abarca la base del conductor.

Descripción.—*Holotipo macho:* Largo total 6.78. Prosoma largo 3.67, ancho 3.07, alto 1.87. Clípeo, alto 0.27. Área ocular largo 1.70, ancho de hilera anterior 2.63, de hilera pos-
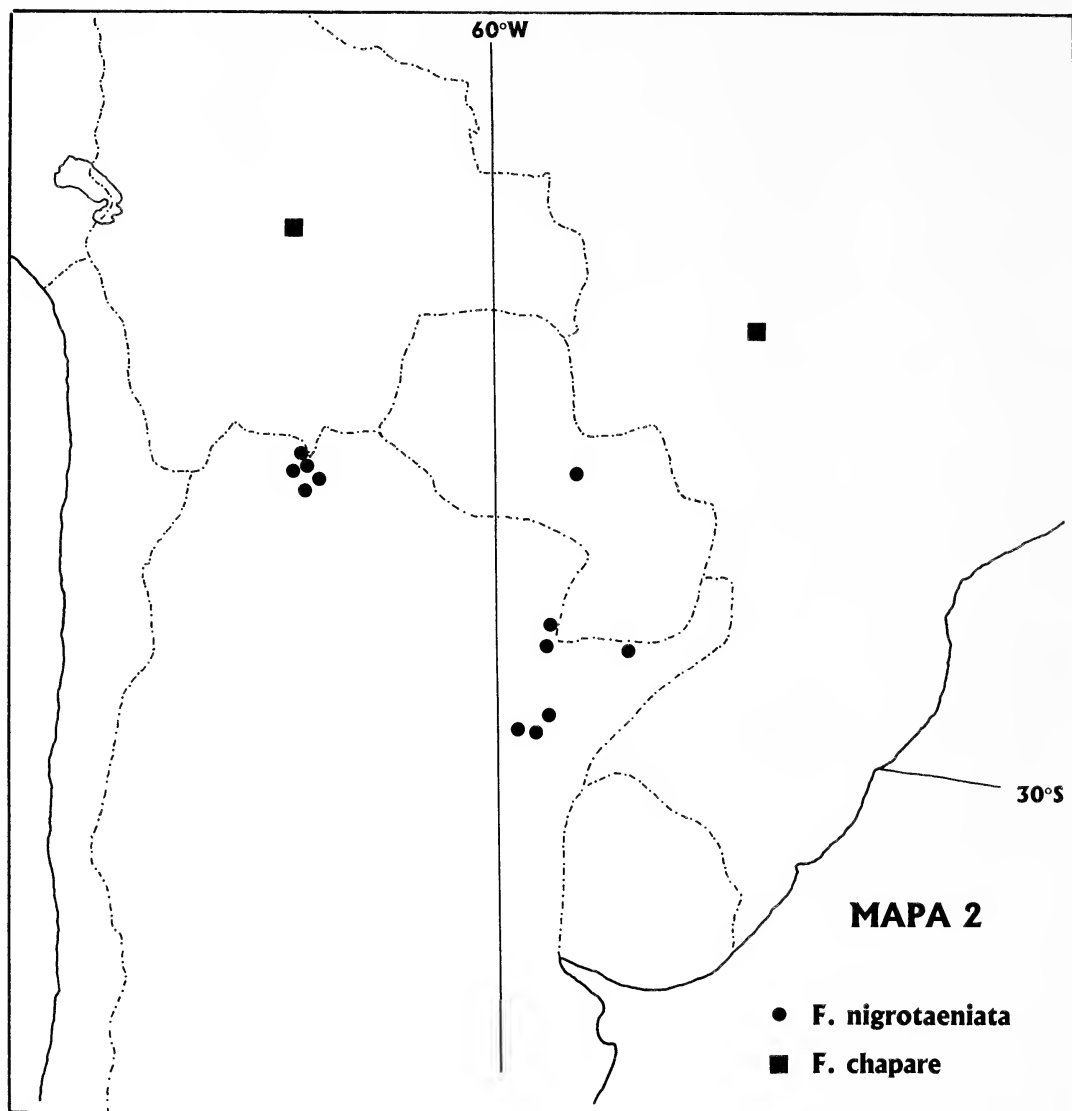
Mapa 2.—Distribución de las especies de *Freya* del grupo *decorata*. América del Sur, aproximadamente entre los paralelos 15°S y 37°S.

terior 2.50. Distancias OLA-OMP 0.43, OMP-OLP 0.40. Diámetro OMA 0.83. Fórmula de patas y quetotaxia como en el género; las tibias III y IV tienen d 1b-2ap. Palpos (Figs. 6, 10, 21, 25, 26, 34): cimbio sin depresión retrodorsal basal; émbolo más grueso y más recto que en *F. decorata;* conductor con ápice curvado, relativamente ancho; base de émbolo y conductor rodeados por un reborde membranoso, que forma una punta visible desde cara retrolateral. Color: como en *F. decorata;* la banda media de pelos blancos en RT puede

haber estado unida a las laterales; banda media longitudinal del opistosoma unida a la basal.

Alotipo hembra: Largo total 9.26. Prosoma largo 3.73, ancho 2.87, alto 1.93. Clípeo, alto 0.23. Área ocular largo 1.53, ancho de hilera anterior 2.50, de hilera posterior 2.47. Distancias OLA-OMP 0.47, OMP-OLP 0.40. Diámetro de OMA 0.80. Fórmula de patas III-IV-I-II. Quetotaxia como en el género. Epigino (Figs. 39, 54, 55): gran escotadura en borde posterior, bolsillos laterales de anclaje bien se-
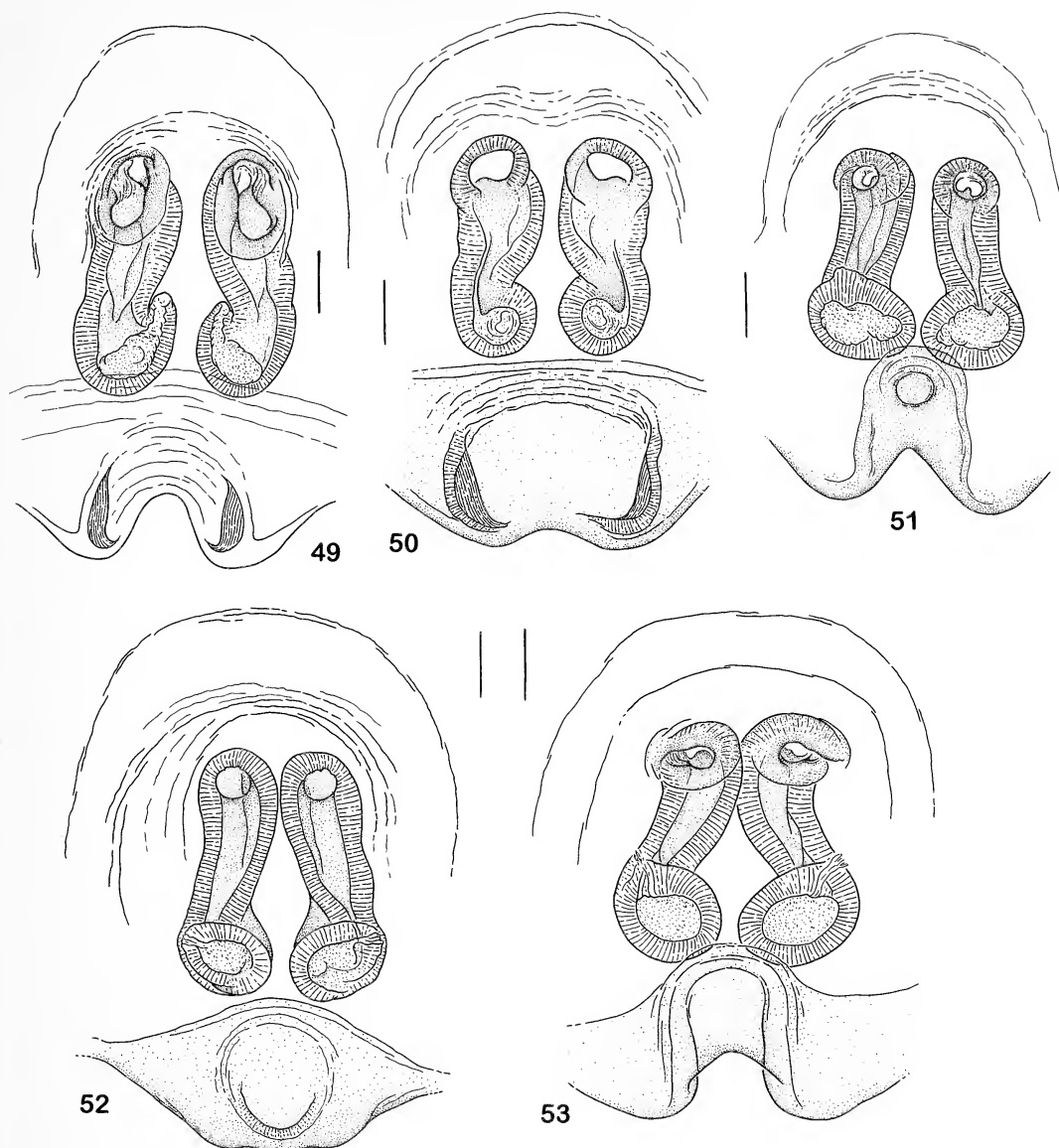
Figuras 49–53.—Epiginos clarificados, vista ventral. 49. *Freya decorata;* 50. *F. rubiginosa;* 51. *F. dureti;* 52. *F. regia;* 53. *F. chapare.* Escalas = 100 μm.

parados. Área anterior media muy granulada, con abundantes rugosidades radiantes; orificios de copulación elípticos, oblicuamente situados, con margen anterior poco marcado, conductos de copulación bien separados, espermatecas esféricas. Color: como en *F. decorata.* La banda media longitudinal del opistosoma no se une a la basal; dorso entre bandas, con pelos pardo dorado o rojizo. Palpos amarillos, con tarsos algo más oscuros, sin manchas dorsales basales pardas en los artejos.

Distribución.—Sólo de la localidad tipo.

AGRADECIMIENTOS
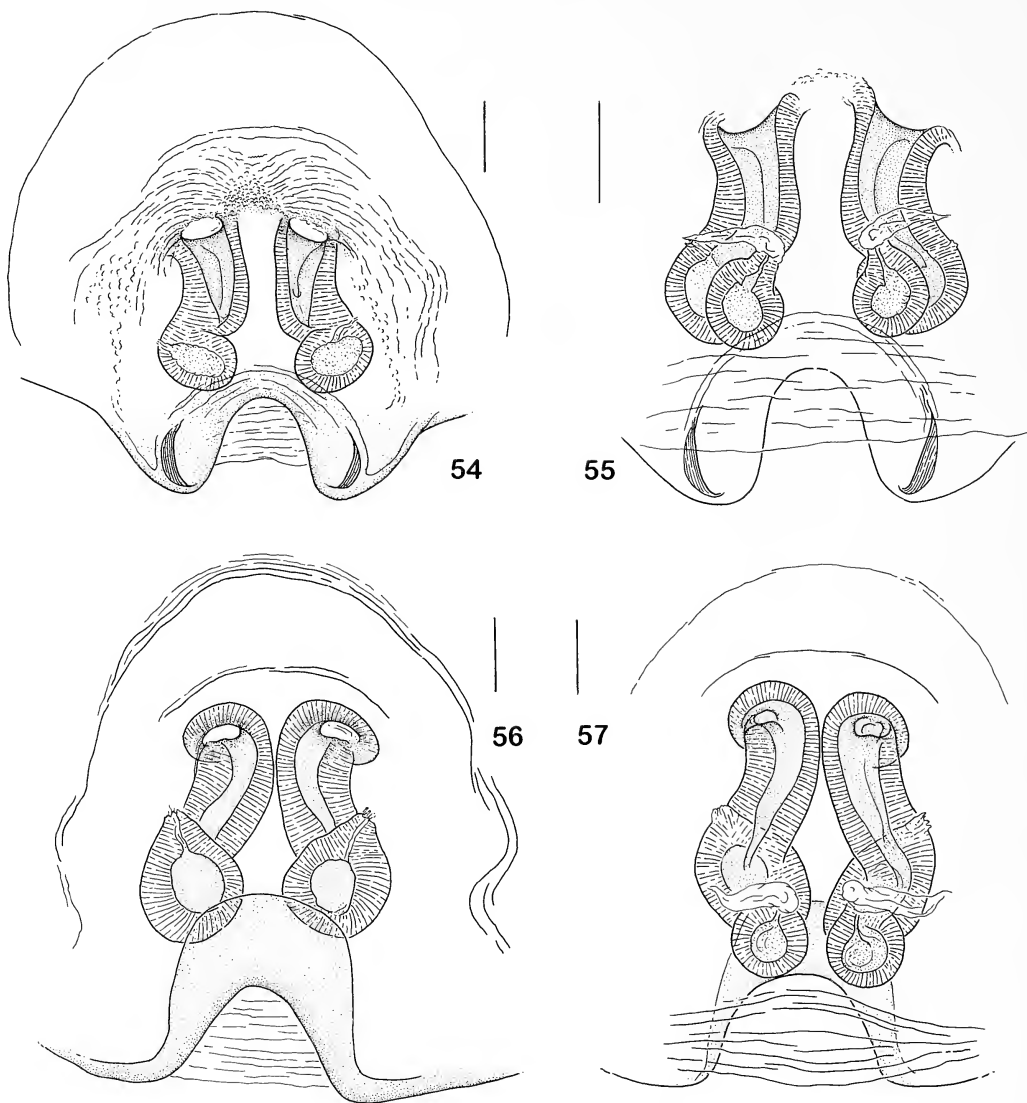
Figuras 54–57.—Epiginos clarificados. 54. *Freya atures,* ventral; 55. El mismo, dorsal; 56. *F. nigrotaeniata,* ventral; 57. El mismo, dorsal. Escalas = 100 μm.

y C.L. Scioscia sus valiosos comentarios sobre el manuscrito. Agradezco a las Técnicas Patricia Sarmiento (MLP) las fotografías de microscopio electrónico de barrido y Susana Ledesma (MACN) la atención de los animales vivos.

LITERATURA CITADA

Bonnet, P. 1955. Bibliographia Araneorum. Toulouse, Vol. 2(1):1–918; 1956, 2(2):919–1925; 1959, 2(5):4231–5058.

Brignoli, P.M. 1983. A Catalogue of the Araneae Described Between 1940 and 1981. 755 pp. Manchester Univ. Press.

Brignoli, P.M. 1985. On the correct dates of publication of the arachnid taxa described in some works by C.W. Hahn and C.L. Koch (Arachnida). Bulletin of the British Arachnological Society, 6(9):414–416.

Cambridge, F.O.P. 1901. Biologia Centrali-Americana. Arachnida. Araneidea and Opiliones, 2: 193–312.

Caporiacco, L. 1938. Aracnidi del Messico, di Guatemala e Honduras Britannico. Atti della Società Italiana di Scienze Naturali, 77:251–282.

Caporiacco, L. 1947. Diagnosi preliminari di specie nuove di arachnidi della Guiana Britannica raccolte dal Professori Beccari e Romiti. Monitore Zoologico Italiano, 56(1–6):16–34.

Caporiacco, L. 1948. Arachnida of British Guiana collected in 1931 and 1936 by Professors Beccari and Romiti. Proceedings of the Zoological Society of London, 118(3):607–747.

Caporiacco, L. 1954. Araignées de la Guyane Française du Muséum d'Histoire Naturelle de Paris. Commentationes, 16(3):45–193. Pontificia Academia Scientiarum.

Chickering, A. 1946. The Salticidae (spiders) from Panama. Bulletin of the Museum of Comparative Zoology 97:1–474.

Galiano, M.E. 1963a. Las variaciones individuales en *Euophrys sutrix* Holmberg, 1874 (Araneae, Salticidae). Revista de la Sociedad Entomológica Argentina, 24:23–28.

Galiano, M.E. 1963b. Las especies americanas de arañas de la familia Salticidae descriptas por Eugène Simon. Redescripciones basadas en los ejemplares típicos. Physis (Buenos Aires) Sec. C, 23(66):230–470.

Galiano, M.E. 1981. Catálogo de los especímenes típicos de Salticidae (Araneae) descriptos por Candido de Mello-Leitão. Segunda parte. Physis (Buenos Aires) Sec. C, 39(97):11–17.

Galiano, M.E. 1982. Revisión del género *Nycerella* (Araneae, Salticidae). Physis (Buenos Aires) Sec. C, 41(100):53–63.

Koch, C.L. 1846. Die Arachniden, 13:1-234. Nürnberg.

Koch, C.L. 1850. Uebersicht des Arachnidensystems, 5:1–104. Nürnberg.

Mello-Leitão, C. 1941. Arañas de la Provincia de Santa Fe colectadas por el Profesor Birabén. Revista del Museo de La Plata, Zoología 2(13):199–225.

Mello-Leitão, C. 1942. Arañas de Chaco y Santiago del Estero. Revista del Museo de La Plata, Zoología, 2(16):381-426.

Mello-Leitão, C. 1945. Arañas de Misiones, Corrientes y Entre Ríos. Revista del Museo de La Plata, Zoología, 4(29):213-302.

Mello-Leitão, C. 1948. Contribução ao conhecimento da fauna Araneológica das Guianas. Annaes da Academia Brasileira de Sciencias, 20(2):151-196.

Neave, S.A. 1939–1940. Nomenclator Zoologicus. A list of the names of genera and subgenera in Zoology from the tenth edition of Linnaeus 1758 to the end of 1935. 2:1–1025, 4:1–758. London.

Peckham, G.W. & E.G. Peckham. 1893. On the Spiders of the Family Attidae of the Island of St. Vincent. Proceedings of the Zoological Society of London, 692–704 pp.

Peckham, G.W. & E.G. Peckham. 1896. Spiders of the Family Attidae from Central America and Mexico. Occasional Papers of the Natural History Society of Wisconsin, 3:1–101.

Penther, Dr. 1900. Beschreibung der *Euophrys decorata* C.L. Koch var. *dyscrita* nov. var. *In* Südamerika gesammelte Myriapoden und Arachnoideen. Zoologischer Anzeiger 23(615):285–286.

Petrunkevitch, A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent Islands, Greenland, West Indies, Terra del Fuego, Galapagos, etc. Bulletin of the American Museum of Natural History 29:1–790.

Petrunkevitch, A. 1928. Systema Aranearum. Transactions of the Connecticut Academy of Arts and Sciences 29:1–270.

Platnick, N.I. 1989. Advances in Spider Taxonomy. 1981–1987. 673 pp. Manchester Univ. Press.

Platnick, N.I. 1993. Advances in Spider Taxonomy. 1988–1991. 846 pp. New York Entomological Society, New York.

Platnick, N.I. 1997. Advances in Spider Taxonomy 1992–1995. With redescriptions 1940–1980. 976 pp. New York Entomological Society, New York.

Platnick, N.I. & M.U. Shadab. 1975. A revision of the spider genus *Gnaphosa* (Araneae, Gnaphosidae) in America. Bulletin of the American Museum of Natural History 155(1):1–66.

Prószyński, J. 1971. Catalogue of Salticidae (Aranei) specimens kept in major collections of the world. Annales Zoologici, Warszawa 28(17):367–519.

Prószyński, J. 1990. Catalogue of Salticidae (Araneae). Synthesis of quotations in the world literature since 1940, with basic taxonomic data since 1758. Wyzsza Skola Rolniczo-Pedagogiczna w Sieldcach. 366 pp. Siedlce (Poland).

Roewer, C.F. 1954. Katalog der Araneae von 1758 bis 1940, bzw. 1954. 2b:925–1751. Brussels.

Simon, E. 1864. Histoire Naturelle des Araignées (Aranéides). 540 pp. Paris.

Simon, E. 1902. Etudes Arachnologiques, 32e Mémoire. Descriptions d'especís nouvelles de la famille des Salticidae. (Suite). Annales de la Societé Entomologique de France 71:389–421.

Simon, E. 1903. Histoire Naturelle des Araignées 2(4):669–1080. Paris.

Taczanowski, L. 1871. Les araneides de la Guyane Française. Trudy rousskago entomologhieskago Obtchiestwa (= Horae Societatis Entomologicae Rossicae) 8:32–132.

Walckenaer, C.A. 1805. Tableau des Aranéides ou Caractères essentiels des tribus, genres, familles et races que renferme le genre Aranea de Linné, avec la désignation des espèces comprises dans chacune de ces divisions. Paris, pp. I–XII, 1–88.

DESCRIPTION OF A NEW SPECIES
IN THE *NITIDULUS* GROUP OF THE GENUS *VAEJOVIS*
(SCORPIONES, VAEJOVIDAE)

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ABSTRACT.   A new species in the *nitidulus* group of *Vaejovis* is described: *V. mauryi* from Sonora, México. Morphological characters, including the hemispermatophore of the holotype male, are illustrated. The species is compared to *Vaejovis decipiens, Vaejovis janssi,* and *Vaejovis intermedius.*

Keywords: Scorpion, Vaejovidae, Sonora, México, taxonomy

Vaejovis is the most diverse genus of scorpions in North America, with 66 described species arranged into five species groups (Sissom 2000). Although a comprehensive revision of the genus is not available at the present time, the genus has recently been catalogued (Sissom 2000). Since the appearance of the catalogue one additional species has been described from Sonora, México (Hendrixson 2001).

The *Vaejovis nitidulus* group is a moderately diverse group with 15 species found from the southern parts of Texas, USA, and through much of México (Sissom & Francke 1985; Sissom 1991; Sissom 2000). Members of the group share the following characteristics: (1) the anterior margin of the carapace is obtusely emarginate, with a distinct median notch; (2) the genital opercula of the female possess a membranous longitudinal connection on the anterior two-thirds to four-fifths; (3) the pectinal teeth of the female are all subequal in size; (4) the ventral submedian carinae of the metasoma are obsolete to moderate and crenulate; (5) the cheliceral movable finger bears a well developed serrula on the ventrodistal aspect; (6) the pedipalps are relatively elongated, with chela length/width ratios greater than 3.3 and usually greater than 4.0; (7) the pedipalp chela fingers in most species terminate in enlarged claw-like denticles bearing an apical white patch; (8) chela trichobothria *ib* and *it* are located at the base of the fixed finger; (9) the denticle row of the pedipalp chela fixed finger is divided into six or seven subrows; (10) the dorsointernal carina of the pedipalp chela is strong and, in most species,

bears enlarged, sharp granules; (11) the ventral spinule row of the telotarsus is flanked distally by a single pair of larger spinules; (12) the male hemispermatophore bears a two-pronged hook at the base of the distal lamina; and (13) the distal margin of the sperm plug is smooth, i.e., devoid of hooks or spines (Sissom & Francke 1985; Sissom 1991).

The only species in the *Vaejovis nitidulus* group previously reported from the state of Sonora, México is *Vaejovis decipiens* Hoffmann 1931; this record is based on two juvenile females (Sissom 1991). While perusing the collections at the California Academy of Sciences, W.D. Sissom found three specimens representing an undescribed species in the *nitidulus* group from this state. These specimens, which were subsequently made available to me for description, were discovered after years of careful examination of museum material from the United States and around the world (Sissom pers. com., September 1999). The rarity of this species in musem collections may be due to its probable lithophilic habits, which make it difficult to collect with conventional rock-rolling techniques.

METHODS

Terminology for general morphology conforms to that of Stahnke (1970) with the following exceptions: terminology for metasomal and pedipalpal carinae is after Francke (1977); and trichobothrial nomenclature follows Vachon (1974), except that the fourth pedipalpal segment is considered the patella rather than the tibia, adhering to Stahnke's terminology.

Vaejovis mauryi new species
(Figs. 1–11)

Type data.—Holotype male, paratype female, and paratype subadult female from Sonora, México, 28°55′N, 109°45′W, 18 September 1982 (V. Roth). Deposited at California Academy of Sciences, San Francisco.

Etymology.—The specific name is a patronym honoring the late Emilio A. Maury for his contributions to the field of arachnology.

Distribution.—Known only from the type locality. According to maps, this locality lies in the vicinity of Mazatán, Bacanora and Soypa in the state of Sonora, México.

Diagnosis.—Within the *nitidulus* group, *Vaejovis mauryi* is most similar to *Vaejovis decipiens* Hoffmann 1931, *V. janssi* Williams 1980, and *V. intermedius* Borelli 1915. It can be easily distinguished from *V. decipiens* and *V. janssi* by (1) the presence in *V. decipiens* and *V. janssi* of ventral submedian carinae on metasomal segments I-II, with these carinae stronger on III-IV; (2) the presence of granulation in the ventral median intercarinal space in *V. mauryi;* (3) weaker digital and external secondary carinae of the pedipalp chelae in *V. mauryi;* (4) the presence in *V. decipiens* and *V. janssi* of strong lateral keels on sternite VII; (5) higher pectinal tooth counts in both *V. decipiens* (22–25 in males, 21–22 in females) and *V. janssi* (21–22 in males, 18–21 in females); and (6) the noticeable difference in size, with *V. mauryi* being smaller.

Vaejovis mauryi can be distinguished from *Vaejovis intermedius* by (1) the sparseness of setation on the pedipalp chelae, metasoma, and sternite VII (in *V. intermedius* these surfaces are very hirsute); (2) the dorsolateral carinae of *V. intermedius* are serrate, whereas those of *V. mauryi* are crenulate; (3) the presence of only weak scalloping in the chela fingers of *V. mauryi* (distinct scalloping in *V. intermedius*); and (4) higher pectinal tooth counts in *V. intermedius* (21–26 in males, 19–23 in females).

Measurements.—Holotype, in mm: total length 35.90; carapace length 4.60; mesosoma length 9.30; metasoma length 17.20. Metasoma: segment I length/width 2.20/2.85; segment II length/width 2.60/2.85; segment III length/width 2.75/2.75; segment IV length/width 3.70/2.65; segment V length/width 5.95/2.35. Telson: length 4.90; vesicle length/depth 3.05/1.8/1.4; aculeus length 1.9. Pedipalps: total length 16.10; femur length/width 4.35/1.25; patella length/width 4.55/1.45; chela length/width/depth 7.20/1.65/1.9; movable finger length 4.60; fixed finger length 3.80.

Description.—Based on holotype. *Coloration (in alcohol):* Base color of carapace and tergites yellow-brown to orange-brown with an underlying dusky pattern. Interocular area darkly pigmented. Metasoma light orange to dark orange. Telson vesicle orange or reddish-brown. Legs orange, with dusky markings proximally; basitarsi and telotarsi uniformly yellow. *Prosoma:* Anterior margin of carapace obtusely emarginate. Median notch shallow. Interocular area finely granular with scattered coarse granules. Remainder densely granular. *Mesosoma:* Median carina on I-II obsolete; on III feeble; on IV-VI weak, granular. On VII, median carina weak, granular; lateral carinae strong, crenulate to serrate, with distal denticle enlarged. Pectinal tooth count 19–19. Sternites III-VI sparsely setose; VII with two weak, finely granular lateral carinae. *Metasoma:* Ratio of segment I length/width 0.76; of segment III length/width 1.00; of segment V length/width 2.50. Segments I-IV: dorsolateral carinae strong, finely crenulate, with distalmost denticle of I slightly enlarged, spinoid; on II-IV distinctly enlarged and spinoid distally. Lateral supramedian carinae on I-III strong, finely crenulate; on IV moderate, granular with distalmost denticles on I-III enlarged and spinoid. Lateral inframedian carinae on I complete, strong, irregularly crenulate; on II present on anterior half as isolated granules, on posterior one-half, weak to moderate, granular to crenulate; on III present on posterior one-third, moderate, finely crenulate; on IV absent. Ventrolateral carinae on I-II moderate, smooth to finely granular; on III-IV moderate, irregularly, finely serratocrenulate. Ventral submedian carinae on I and II obsolete; on III weak, feebly granular; on IV weak, irregularly granular. Dorsal and lateral intercarinal spaces sparsely, coarsely granular. Ventromedian intercarinal space on IV granulose. Setal count on segments I-IV: dorsolateral setae 0/0:1/1:1/1:2/2; lateral supramedian setae 1/1:2/1:2/2:3/3; lateral inframedian setae 2/2:1/1:1/1:0/0; ventrolateral setae 3/3:3/3:3/3:4/4; ventral submedian setae 3/3:4/4:4/4:4/4. Segment V: (Fig. 1) Dorsolateral carinae moderate, cren-
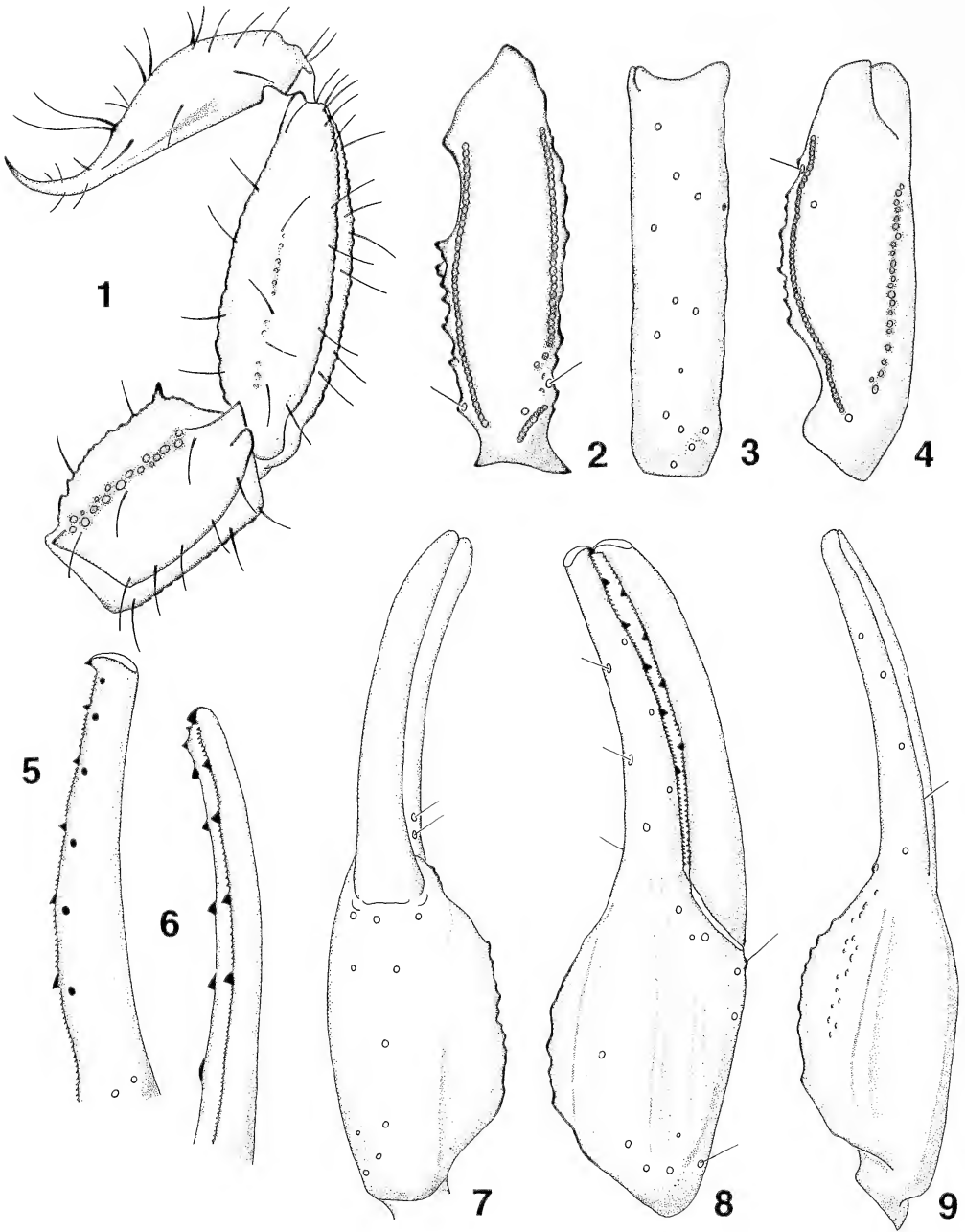
Figures 1–9.—Morphology of *Vaejovis mauryi* (all drawings of holotype male). 1. Lateral view of metasomal segments IV and V and the telson; 2. Dorsal aspect of pedipalp femur; 3. External aspect of pedipalp patella; 4. Dorsal aspect of pedipalp patella; 5. Dentition of pedipalp chela fixed finger; 6. Dentition of pedipalp chela movable finger; 7. Ventral aspect of pedipalp chela; 8. External aspect of pedipalp chela; 9. Dorsal aspect of pedipalp chela.

ulate basally, granular distally. Lateromedian carinae weak, granular, present on anterior 3/4. Ventrolateral carinae strong, serrate. Ventromedian carina strong, crenulate. Intercar-inal spaces with scattered, coarse granules. Segment V setal count: dorsolateral setae 5/6; lateromedian setae 4/4; ventrolateral setae 7/9. *Telson:* (Fig. 1) Ventral aspect with irreg-

ular punctations and granulation. Ventral midline with small granules terminating in a subtle subacular tubercule. Nine pairs of large setae, with several smaller setae. *Pedipalps:* Trichobothrial pattern type C, orthobothriotaxic. Pedipalpal ratios: chela length/width 4.20; femur length/width 3.38; fixed finger length/carapace length 0.83. Femur: (Fig. 2) carinae strong, granulose; internal face with 8–10 large, pointed granules, with scattered fine granules. Patella: (Figs. 3, 4) Dorsointernal, ventrointernal, and ventroexternal carinae strong, crenulate. Internal face with oblique longitudinal carina of 8 large, serrated granules and 10 smaller granules. Chela: (Figs. 7, 8, 9) Dorsal marginal carina strong, crenulate. Dorsal secondary carina moderate, smooth. Digital carina moderate, smooth. External secondary carina weak, smooth. Ventroexternal carina moderate, granular. Ventromedian carina vestigial. Ventrointernal carina moderate, smooth. Dorsolateral carina strong, with large, crenulate granules. Dentate margin of fixed finger (Fig. 5) with primary denticle row divided into six subrows by five enlarged denticles; six inner accessory granules. Dentate margin of chela movable finger (Fig. 6) with primary denticle row divided into six subrows by five enlarged denticles; seven inner accessory granules. Fingers without distinct scalloping. *Hemispermatophore:* (Figs. 10, 11) Distal lamina slightly longer than trunk, not distinctly tapered. Median lobe relatively large, rounded.

Variation.—Only three specimens were available for study. These included one adult male, one adult female, and one subadult female. The adult female is better preserved than the male and may therefore be closer to the actual coloration of the species. Base color of carapace and tergites deep orange-brown to yellow-brown with underlying dusky pattern. Metasomal segment V slightly darker than the preceding segments. Legs yellow-brown with mottling proximally; basitarsi and telotarsi uniformly yellow. Interocular area of female smooth with scattered coarse granules. Remainder of prosoma sparsely granular. Ventrolateral carinae smooth to finely granular on I-II; moderate, finely serrate on III-IV. Ventrolateral carinae in juvenile female paratype moderate, finely serrate on I-II; moderate, irregularly serratocrenulate to finely serrate on
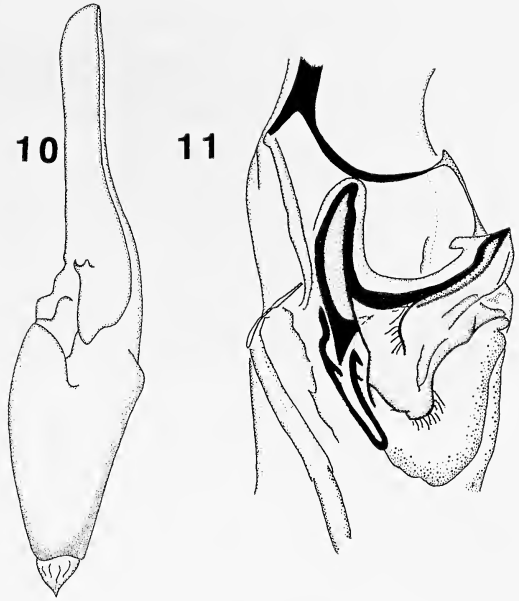
Figures 10–11.—Morphology of the hemispermatophore of *Vaejovis mauryi* (holotype male). 10. Dorsal aspect of left hemispermatophore; 11. Capsular area of left hemispermatophore.

III-IV. Pectinal tooth count 17–17 in both female paratypes.

Selected measurements (in mm) of the paratype female are as follows: total length 40.60; carapace length 5.70; mesosoma length 12.25; metasoma length 17.30; metasoma segment III length/width 2.70/3.05; segment V length/width 6.45/2.80; chela length/width/depth 8.95/1.85/2.10; fixed finger length 4.90; movable finger length 5.95.

Setal counts of the adult and subadult females are as follows (L/R): Dorsolaterals: 0/0:1/1:1/1:2/2 and 0/0:1/1:1/1:2/2. Lateral supramedians: 0/1:2/1:2/1:4/4 and 0/0:1/1:2/2:3/3. Lateral inframedians: 2/3:1/1:0/1:0/0 and 2/2:1/1:0/0:0/0. Ventrolaterals: 2/2:3/3:3/4:5/5 and 3/3:3/3:3/3:4/3. Ventral submedians: 3/3:4/4:4/4:4/5 and 3/3:4/4:4/4:4/4. Setal counts on V are as follows: dorsolaterals: 2/5 and 5/5; lateromedians: 3/4 and 4/4; ventrolaterals: 8/7 and 7/8.

Specimens examined.—MÉXICO: Sonora, 28°55'N, 109°45'W, (pine forest which, according to maps of the area, must be located between Mazatán, Bacanora, and Soyopa), 18 September 1982 (V. Roth), 1 male holotype, 1 female paratype, 1 juvenile paratype (CAS).

LITERATURE CITED

Francke, O.F. 1977. Two emendations to Stahnke's (1974) Vaejovidae revision (Scorpionida, Vaejovidae). Journal of Arachnology 4:125–135.

Hendrixson, B.E. 2001. A new species of *Vaejovis* (Scorpiones, Vaejovidae) from Sonora, Mexico. Journal of Arachnology 29:47–55.

Hoffmann, C.C. 1931. Los scorpiones de México. Primera parte: Diplocentridae, Chactidae, Vejovidae. Anales del Instituto de Biología de la Universidad Nacional Autónoma de México 8:291–408.

Sissom, W.D. 1991. Systematic studies on the *nitidulus* group of the genus *Vaejovis,* with descriptions of seven new species (Scorpiones, Vaejovidae). Journal of Arachnology 19:4–28.

Sissom, W.D. 2000. Family Vaejovidae Thorell, 1876. Pp. 503–553. *In* Catalog Of The Scorpions Of The World (1758–1998). (V. Fet, et al., eds.). New York Entomological Society.

Sissom, W.D. & O.F. Francke. 1985. Redescriptions of some poorly known species of the *nitidulus* group of the genus *Vaejovis* (Scorpiones, Vaejovidae). Journal of Arachnology 13:243–266.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. Entomological News 81:297–316.

Vachon, M. 1974. Étude des caráctères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie, Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. Bulletin du Muséum National d'Histoire Naturelle, Paris, (Sér. 3), 140 (Zool. 104), mai-juin 1973:857–958.

A NEW SPECIES OF *VAEJOVIS*
(SCORPIONES, VAEJOVIDAE) FROM SONORA, MEXICO

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ABSTRACT. *Vaejovis pequeno,* a new species of scorpion previously confused with *V. waueri* Gertsch & Soleglad 1972, is described and illustrated from Sonora, Mexico and is compared to that species. A revised diagnosis and new distributional records for *V. waueri,* a member of the *eusthenura* group, are provided.

Keywords: Scorpion, Vaejovidae, Sonora, Mexico, systematics

Vaejovis is the most diverse genus of scorpions in North America with 66 described species and five recognized species groups (i.e., *eusthenura, intrepidus, mexicanus, nitudulus* and *punctipalpi;* Sissom 2000). To date, there is no single comprehensive revision of the genus, but a number of partial revisions and regional faunas can be found in the literature (Williams 1970a, 1970b, 1971, 1980; Soleglad 1973; Sissom & Francke 1985; Sissom 1991a; Capes 2001).

Gertsch & Soleglad (1972) described a small, attractive scorpion, *Vaejovis waueri,* on the basis of specimens from southern Texas in the USA, and from the states of Nuevo León and Sonora in Mexico. This species is well known in the eastern regions (i.e., Texas and Nuevo León), but the Sonoran record from Rio Cuchajaqui represents a significant disjunction. Sissom (1991b) suggested that humans may have accidentally introduced the species to Sonora, supported by the fact that no additional specimens had been collected from the well-sampled Alamos area in the southeastern corner of the state. At the time, only subtle differences in morphology were detected between the specimens from Sonora and Texas including slight variations in the ventrolateral carination of metasomal segment V. My findings, based on subsequent examination of the Rio Cuchajaqui material and some new material that has since accumulated, indicate that these specimens are distinct from *V. waueri* and represent a new species.

The superficial resemblance between the new species and *V. waueri* is striking, so it is understandable that the earlier authors believed these Sonoran specimens to be *V. waueri,* despite the disjunction. Both of these diminutive species possess relatively lustrous cuticles and exhibit similar color patterns (e.g., dusky, mottled appearance with lighter medial stripe), morphometrics, and carination. In addition to describing the new species and comparing it to *V. waueri,* it is my purpose here to provide a revised diagnosis for *V. waueri* and to review the species distribution based on many new records.

METHODS

Nomenclature and mensuration for the most part follow that of Stahnke (1970), with the following exceptions: carinal terminology is after Francke (1977) and trichobothrial terminology is after Vachon (1974), except that the fourth pedipalpal segment is considered the patella rather than the tibia, adhering to Stahnke's nomenclature. Morphometric characters were derived from measurements of a single adult male and nine adult females for the new species, and from 10 adult males and 10 adult females for *V. waueri;* several ($n >$ 50) additional adult *V. waueri* were used to provide a revised diagnosis for that species. Hemispermatophore preparation follows that of Sissom et al. (1990). All measurements were taken using an ocular micrometer calibrated at $20\times$, and illustrations were carried out by the use of an ocular grid.

Specimen depository designations are as follows: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANS); Appalachian State University, Boone, North Carolina
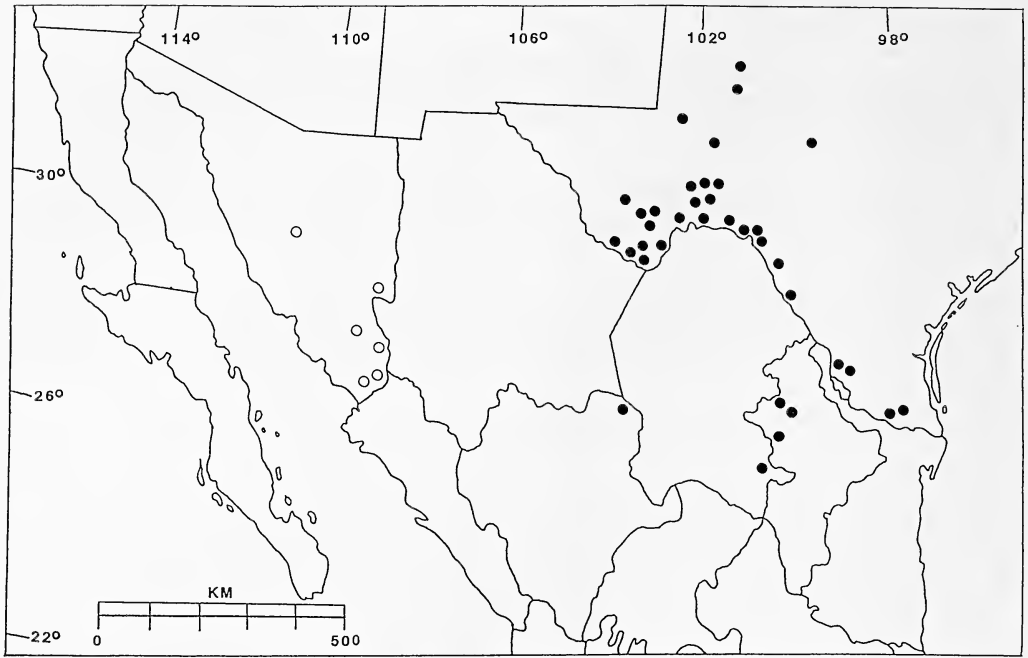
Figure 1.—Map of the southwestern United States and northern Mexico depicting the distribution of *Vaejovis pequeno* new species (○) and *V. waueri* (●).

(ASU); Florida State Collection of Arthropods, Gainesville (FSCA); California Academy of Sciences, San Francisco (CAS); personal collection of J. A. Nilsson (JAN); University of Arizona, Tucson (UA); University of Arkansas, Fayetteville (UAF); personal collection of W. David Sissom (WDS); West Texas A&M University, Canyon (WTAMU).

Vaejovis pequeno new species
Figs. 1, 2, 4–15

Vejovis waueri, in part: Gertsch & Soleglad 1972: 607 (misidentification).
Vaejovis waueri: Sissom 1991b: 215 (misidentification).

Type data.—Adult male holotype collected 15 mi W Yecora (4000 feet) (1200 m), Sonora, Mexico on 7 August 1986 by V. Roth; deposited at the California Academy of Sciences, San Francisco. For paratype data, see "Specimens examined" section.

Etymology.—The specific epithet comes from the Spanish *pequeño* (meaning "little one") and refers to the minute size of this species; *pequeno* is regarded as a noun in apposition.

Distribution.—Known from several localities in Sonora, Mexico (Fig. 1).

Diagnosis.—*Vaejovis pequeno* (Fig. 2) may be distinguished from *V. waueri* by being somewhat smaller in size (adults of *V. pequeno* to 19.85 mm and *V. waueri* to 24.8 mm); possessing weak, granular dorsal marginal and dorsointernal carinae on the pedipalp chelae in males (rather than all keels obsolete); the inner lobe of the hemispermatophoric capsule without barbs (rather than distinctly barbed); the chelicerae with a strongly developed serrula (rather than a weakly developed serrula); one pair of distal spinules flanking the ventromedian spinule row of the tarsi (rather than more than one pair); consistently lower setal counts on the metasoma (see Figs. 3, 4); and finely granular to weak, serrate ventral submedian carinae on metasomal segment IV (rather than obsolete). The holotype male can be differentiated from *V. waueri* males (*n* = 10) by the following morphometric ratios (*V. waueri* ratios in parentheses; slightly overlapping ratios have been included): pedipalp femur length/width 2.82 (2.46–2.82), carapace length/metasomal segment V length 1.00 (0.80–0.90), and chela fixed finger length/carapace length 0.59 (0.50–0.56). The paratype females (*n* = 9) can be differentiated from *V. waueri* females (*n* = 10) by the fol-

Figure 2.—Photograph showing dorsal view of paratype female (left) and holotype male of *Vaejovis pequeno* new species. Photograph by W.D. Sissom.

lowing morphometric ratios: pedipalp femur length/width 2.60–3.00 (2.41–2.60), chela movable finger length/chela length 0.60–0.63 (0.56–0.60), carapace length/metasomal segment V length 1.00–1.04 (0.90–0.98), and chela fixed finger length/carapace length 0.58–0.65 (0.50–0.56).

The placement of *V. pequeno* in an existing species group is problematic as its closest relative is unknown. Although superficially similar to *V. waueri,* a member of the *eusthenura* group as defined by Williams (1970b), *V. pequeno* clearly does not belong to that group based on the chelicerae possessing a strongly pronounced serrula, one pair of distal spinules flanking the ventromedian spinule row of the tarsi, and the absence of barbs on the capsule of the hemispermatophore. In addition, species of the *eusthenura* group that possess strong mottling and fairly robust metasomal segments [e.g., *V. waueri, V. bilineatus* Pocock 1898, *V. spinigerus* (Wood 1863), and *V. gravicaudus* Williams 1970], all have extremely setose metasomal carinae.

Vaejovis pequeno is also superficially sim-

ilar to *Serradigitus agilis* Sissom & Stockwell 1991 of northern Sonora and southern Arizona, but does not possess the synapomorphies associated with that genus. In particular, *V. pequeno* does not bear serrated denticle rows on the pedipalp chela fingers, enlarged terminal denticles on the chela fingers, or enlarged proximal pectinal teeth devoid of sensilla in the female. Further, *S. agilis* has higher pectinal tooth counts than *V. pequeno* (14–17 in males instead of 12–13, and 14–15 in females instead of 11–13); and finally, trichobothria *ib* and *it* flank the sixth inner accessory denticle on the chela fixed finger in *S. agilis,* but *it* is slightly basal to the sixth inner accessory denticle in *V. pequeno.*

Description.– Based on adult male holotype (Fig. 2). *Coloration (in alcohol):* Base color orange-yellow to orange with underlying dusky pattern. Mesosomal dorsum with distinct medial, longitudinal stripe. Metasomal segments progressively darker distally from yellow-orange to reddish-brown. Telson yellow-orange; aculeus orange-red. Ventral surface cream colored. Pedipalp chela with dusky longitudinal stripes marking positions where keels generally occur. Legs yellow with some dusky mottling. *Prosoma:* Anterior edge of carapace slightly emarginate. Carapace surface densely, finely granular. *Mesosoma:* Sternite VII with weak, serrate lateral keels. Tergites densely, finely granular. Pectinal tooth count 13/12 (l/r). *Metasoma:* (Fig. 4) Segments I-III wider than long, IV longer than wide, V 1.76 times longer than wide. Segments I-IV: intercarinal regions finely to coarsely granular. Dorsolateral and lateral supramedian carinae strong, crenulate to serrate terminating in an enlarged, spinoid tubercle (except on lateral supramedians of IV, which are widely flared). Lateral inframedian carinae on I moderate, crenulate; on II-III weak to moderate, granular to crenulate; on IV absent. Ventrolateral carinae on I weak to moderate, crenulate; on II-III moderate, crenulate; on IV strong, crenulate. Ventral submedian carinae on I obsolete; II-III weak, smooth to granular; on IV weak, serrate. Segment V: intercarinal regions finely to coarsely granular. Dorsolateral carinae strong, irregularly crenulate. Lateromedian carinae moderate to weak, granular. Ventrolateral and ventromedian carinae strong, crenulate to serratocrenulate. Segments I-IV carinal setation (l/r): dorsolaterals,

1/0:1/1:1/1:2/2; lateral supramedians, 0/0:1/1:
1/1:2/3; lateral inframedians, 1/1:0/0:0/0:0/0;
ventrolaterals, 2/2:3/3:3/3:3/3; ventral subme-
dians, 3/3:3/3:3/3:3/3:3/4. Segment V carinal se-
tation: dorsolaterals, 5/5; lateromedians, 3/3;
ventrolaterals, 5/5; ventromedians: 5/5. *Tel-
son:* (Fig. 4) Surface smooth to weak, granu-
lar; moderately setose. Vesicle dorsoventrally
compressed, flattened dorsally. Subaculear tu-
bercle minute, rounded and flanked by two
large setae. *Pedipalps:* Orthobothriotaxic,
Type C (Vachon 1974). All surfaces densely,
finely granular. Femur (Fig. 5) tetracarinate:
moderate, granular to crenulate. Patella (Figs.
6, 7) with dorsointernal and ventrointernal ca-
rinae moderate, granular; internal carinae
moderate, irregularly crenulate; dorsoexternal
carinae weak, smooth to irregularly granular;
ventroexternal carinae smooth. Chela (Figs. 8,
9) with finely granular dorsal marginal and
dorsointernal carinae; others obsolete. Fixed
finger (Fig. 10) with primary denticle row di-
vided into five subrows by four enlarged pri-
mary row denticles; six inner accessory den-
ticles present; trichobothria *ib* and *it* situated
just basal to sixth inner accessory denticle.
Movable finger (Fig. 11) with primary denti-
cle row divided into six subrows by five en-
larged primary row denticles; seven inner ac-
cessory denticles present. Cutting margin of
both fingers straight (i.e., not scalloped). *Hem-
ispermatophore:* (Figs. 12–15) Distal barb of
mating plug without hooklets; distal flange
present.

Measurements of male holotype: (mm) To-
tal L, 14.55; carapace L, 2.20; mesosoma L,
3.35; metasoma L, 6.90; telson, 2.10. Meta-
somal segments: I L/W, 0.90/1.35; II L/W,
1.10/1.20; III L/W, 1.10/1.25; IV L/W, 1.60/
1.25; V L/W,2.20/1.25. Telson: vesicle L/W/
D, 1.30/1.10/0.60; aculeus L, 0.80. Pedipalps:
total L, 6.00; femur L/W, 1.55/0.55; patella L/
W, 1.80/0.70; chela L/W/D, 2.65/0.65/0.65;
fixed finger L, 1.45; movable finger L, 1.55.

*Measurements of female paratype from Ye-
cora:* (mm) Total L, 17.55; carapace L, 2.65;
mesosoma L, 4.65; metasoma L, 7.85; telson,
2.40. Metasomal segments: I L/W, 1.10/1.65;
II L/W, 1.25/1.50; III L/W, 1.30/1.50; IV L/W,
1.65/1.40; V L/W,2.55/1.45. Telson: vesicle L/
W/D, 1.50/0.95/0.75; aculeus L, 0.90. Pedi-
palps: total L, 7.30; femur L/W, 1.90/0.75; pa-
tella L/W, 2.15/0.85; chela L/W/D, 3.20/0.80/

0.85; fixed finger L, 1.55; movable finger L,
2.00.

Variation.—The single adult male differed
from nine adult females in the following re-
spects: body size is somewhat smaller (17.55–
19.85 mm in females) and the carination of
the pedipalp chela is more pronounced (weak,
smooth to irregularly granular in females). In
addition, the holotype male can be differenti-
ated from the paratype females by the follow-
ing morphometric ratios (female ratios in pa-
rentheses; slightly overlapping ratios have
been included): chela movable finger length/
chela length 0.58 (0.60–0.63) and carapace
length/metasomal segment V length 1.00
(1.00–1.04). Pectinal tooth counts of the ho-
lotype male fell within the range of nine par-
atype females: 13/12 (l/r) pectinal teeth in the
male, 11–13 (mode = 12) in females. Addi-
tional male material is needed to determine if
pectinal tooth counts are significantly different
between males and females.

The following morphometric ratio ranges
have been included to indicate intraspecific
variation within the females (mean ± one
standard deviation): chela length/width 3.81–
4.62 (4.00 ± 0.28), pedipalp femur length/
width 2.60–3.00 (2.74 ± 0.13), metasomal
segment III length/width 0.81–0.93 (0.87 ±
0.04), and metasomal segment V length/width
1.61–1.80 (1.67 ± 0.07).

Metasomal carination slightly variable in
strength of the keels; however, the difference
was not determined to be significant. Meta-
soma carinal setation proved to be somewhat
variable. Variation on segments I-IV is as fol-
lows: dorsolaterals, 0-1:1:1:2; lateral supra-
medians, 0-2:1-4:1-4:2-4; lateral inframedi-
ans, 1-2:0-1:0-1:0 (sometimes accessory setae
were present where the lateral inframedian
keel would be located); ventrolaterals, 2-3:3:
3:3-4; ventral submedians, 3:3:3:3-4. Segment
V carinal setation: dorsolaterals, 5; laterome-
dians, 3-5; ventrolaterals, 5; ventromedians, 5.
One female possessed five (instead of the typ-
ical six) inner accessory denticles on the ped-
ipalp chela fixed finger.

Specimens examined.—MEXICO: *Sonora:* 15–20
km E Baviacora (29.43N, 110.05W), 6 August, no
year (V. & B. Roth), 1 paratype female (CAS); Rio
Cuchajaqui, E of Alamos, 14 January 1968 (V.
Roth), 2 paratype females (AMNH); 7 mi NE Teso
Paco (28.50N, 109.40W; thorn forest), 16 Septem-
ber 1982 (V. Roth), 3 paratype females + 18 first
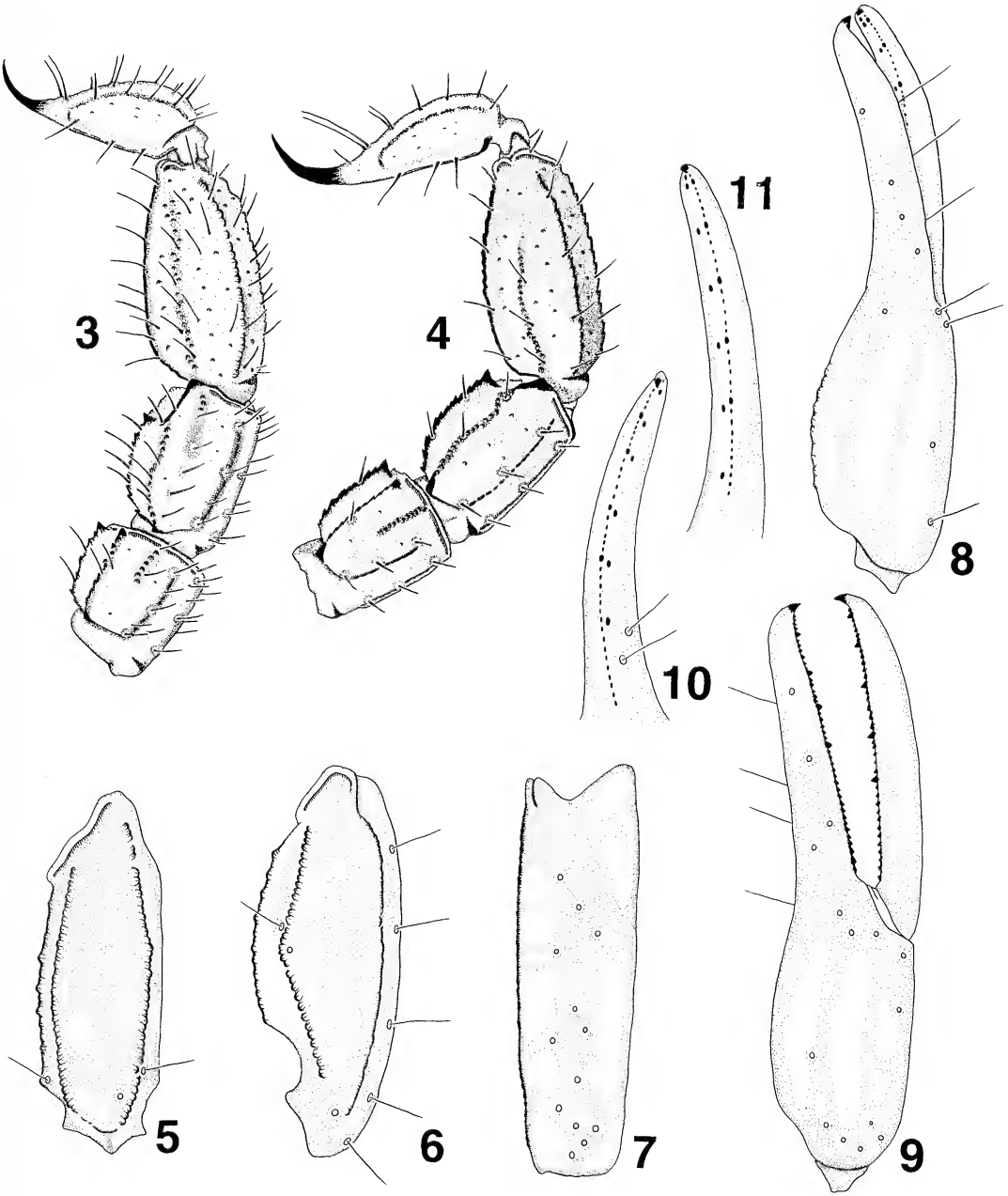
Figures 3–11.—3. External morphology of *Vaejovis waueri,* female from San Angelo, Texas. Metasomal segments III-V and telson, showing carinal setal pattern, lateral aspect. 4–11. External morphology of **Vaejovis pequeno** new species, holotype male from Yecora, Sonora, Mexico; 4. Metasomal segments III-V and telson, showing carinal setal pattern, lateral aspect; 5. Pedipalp femur, dorsal aspect; 6. Pedipalp patella, dorsal aspect; 7. Pedipalp patella, external aspect; 8. Pedipalp chela, dorsal aspect; 9. Pedipalp chela, external aspect; 10. Pedipalp chela fixed finger, showing dentition and trichobothrial pattern; 11. Pedipalp chela movable finger, showing dentition.
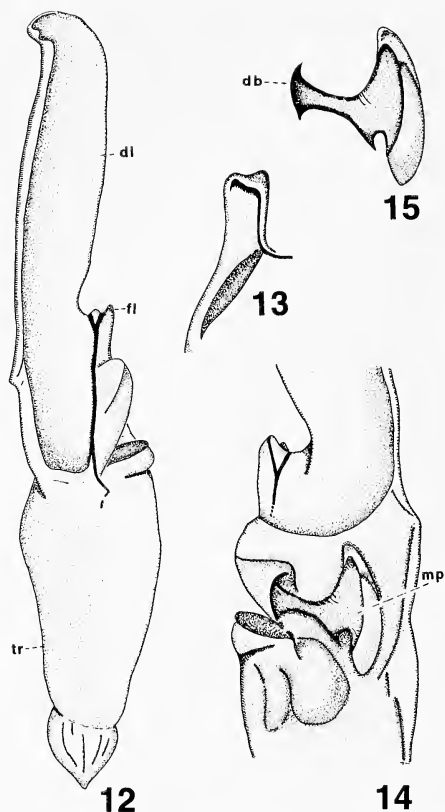
Figures 12–15.—Morphology of right hemispermatophore of **Vaejovis pequeno** new species. 12. Dorsal aspect; 13. Enlarged view of flange; 14. Ventral aspect showing capsule; 15. Mating plug (note the absence of hooklets on distal barb). *Abbreviations:* db = distal barb of mating plug; dl = distal lamina; fl = flange; mp = mating plug; tr = trunk.

instar young (CAS); 15 mi W Yecora (4000 feet), 7 August 1986 (V. Roth), 1 holotype male 1 paratype female (CAS); 3.2 mi NW Huicochi (under rocks; 5200 feet), 11–14 June 1989 (S. Prchal), 1 paratype female + 11 second instar young (WDS); Sierra Alamos above La Cieneguilla (1600–2000'), 11 October 1994 (P.H. Holm), 1 paratype female (UA).

Vaejovis waueri Gertsch & Soleglad
Figs. 1, 3

Vejovis waueri: Gertsch & Soleglad 1972: 605, fig. 145, 146.

Vaejovis waueri was originally described as a member of the *spinigerus* group by Gertsch & Soleglad (1972); however, *V. spinigerus* and its close relatives were actually placed in the *eusthenura* group by Williams (1980), and are still assigned there (Sissom 2000).

Diagnosis.—For characters separating *V. pequeno* from *V. waueri,* see diagnosis for *V. pequeno. Vaejovis waueri* is most closely related to *V. bilineatus* in the *eusthenura* group, but can be differentiated from that species by the following characters (*V. bilineatus* characters in parentheses; Yahia & Sissom 1996): somewhat smaller size, adults to 24.8 mm (22–32 mm); ventral submedian carinae of metasomal segments I-IV always obsolete (sometimes weak, crenulate on IV); a single dorsomedial stripe (two or four); modal pectinal tooth counts 14 in males, 12 in females (17 in males, 15 in females); metasomal segment V length width 1.67–1.90 in males, 1.62–1.84 in females (2.00–2.38 in males, 1.78–2.18 in females); and male chela fingers with cutting margin straight (moderately scalloped).

Distribution.—*Vaejovis waueri* was previously recorded from Texas in the USA (Gertsch & Soleglad 1972; Stockwell 1986) and from Nuevo León and Durango in Mexico (Sissom 2000). The current distribution, including old and new records, is shown in Fig. 1. This species has been collected between roughly 1000–2000 m in the Big Bend area of Texas where it is almost always located on rocky, boulder-strewn slopes. It is not known to burrow, but likely inhabits cracks and crevices among boulders and rocks during the day.

Stockwell (1986), in an unpublished Master's thesis, listed the following localities from Texas: *Brewster County:* Alpine, 8 mi S Alpine, 4 mi W Marathon, 21 mi S Marathon, Big Bend National Park (N base of Grapevine Mt., base of Nugent Mt., K-Bar Road, Chisos Basin Pass, Chisos Mts., Chisos Basin, Rio Grande Village, Bouquillas Canyon); *Crockett County:* 10 mi N Iraan, 11 mi N Iraan, 45 mi NW Ozona, 22 mi E Iraan; *Crosby County:* 24 mi SE Crosbyton; *Garza County:* 7 mi ENE Justiceberg, 3 mi S Justiceberg; *Jeff Davis County:* Davis Mts. State Park, Fort Davis, 1.2 mi SW Hwy 17 on Hwy 1832; *Kinney County:* 21 mi N Brackettville, Brackettville; *Maverick County:* 7 mi S Spofford, 14 mi S El Indio; *Pecos County:* 12 mi N Ft. Stockton, 4 mi E Sheffield, 4 mi SE Sheffield, 52.5 mi NW Dryden, 15 mi N Sanderson; *Starr County:* Rio Grande City; *Terrell County:* 19 mi S Sheffield, Chandler Ranch, 5 mi N Sanderson,

72 mi W Pecos River on Hwy 90; *Val Verde County:* 21 mi N Comstock, 14 mi N Comstock, 0.5 mi S Langtry; *Webb County:* 45 mi S El Indio, Laredo.

New records.—UNITED STATES: Texas: *Brewster County:* Big Bend National Park (BBNP), Chisos Basin (W face of Casa Grande), 29 August 1984 (Sissom et al.) 1♂ 1♀ (WDS); BBNP, Chisos Basin, 28 Sept 1950 (Gertsch), 1♂6♀ (AMNH); BBNP, Chisos Basin, 5 August 1938 (Mulaik), 1♂6♀ (AMNH); BBNP, Chisos Basin, 28 September 1950 (Gertsch), 2♂1♀ (AMNH); BBNP, Chisos Basin, 28 May 1952 (no collector), 18♀ (AMNH); BBNP, Chisos Basin, 26 July 1938 (Mulaik), 1♀ (AMNH); BBNP, Chisos Basin, 16 July 1921 (Duncan), 1♀ + young (AMNH); BBNP, Chisos Basin, 28 September 1950 (no collector), 2♀ (AMNH); BBNP, Chisos Basin (6000'), 25 August 1967 (Gertsch & Hastings), 2♂1♀ (AMNH); BBNP, Chisos Basin, 22 August 1959 (McAlister), 1♀ (AMNH); 10 mi N Hot Springs on Marathon Rd., 21 July 1938 (Mulaik) 1♀ (AMNH); BBNP, Hot Springs parking lot and trail to Hot Springs, 24 June 1998 (Henson et al.), 1♂ (ASU, Q-283A); BBNP, Basin, May 1983 (Henson), 1♀ (ASU, G-119, 1091); BBNP, Pine Canyon Trail-Grassland, 24 May 1987 (Henson et al.), 1♀ (ASU, A-94, 0092); BBNP, Lost Mine Trail, 23 May 1987 (Henson et al.), 1♀ (ASU, A-61, 0059); BBNP, Pine Canyon Road, 24 May 1987 (Henson et al.), 1♀ (ASU, A-83); BBNP, Pine Canyon, end of wooded area to parking lot, 27 May 1992 (no collector), 1♀ (ASU, L-203); BBNP, Pine Canyon, end of wooded area to parking lot, 27 May 1992 (no collector), 1♀ (ASU, L-205, 1916); BBNP, Dugout Wells, 19 May 1987 (Henson et al.), 1♀ (ASU, A-7, 0007); BBNP, Window Trail, 26 May 1987 (Henson et al.), 1♀ (ASU, A-118); BBNP, Glenn Spring Road, 19 May 1988 (Henson), 1♀ (ASU, B-2-a-1, 0248); BBNP, Pine Canyon Trail, edge of grassland and piñon pine, 24 May 1987 (Henson et al.), 1♀ (ASU, A-77, 0075); BBNP, Window Trail below group campground, 23 May 1987 (Henson), 1♀ (ASU, A-58, 0057); BBNP, Basin, May 1983 (no collector), 1 juv. ♀ (ASU, G-117, 1089); BBNP, Mine Trail (6350'), 9 June 1991 (Henson et al.), 1♀ (ASU, H-273, 1459); BBNP, end of Grapevine Hill Road near Grapevine Spring, 31 May 1990 (Henson & David), 1♀ (ASU, D-143, 0519); BBNP, Pine Canyon Trail above parking area, 27 May 1992 (Van Devender), 4♀ (ASU, L-292-295, 2009-2012); BBNP, Window Trail, 20 May 1988 (Henson), 1♀ (ASU, B-4-d-1, 0333); BBNP, Glenn Spring Road, 19 May 1988 (Henson), 1♀ (ASU, B-2-d-1, 0264); BBNP, Window Trail, 20 May 1988 (Henson), 1♀ (ASU, B-4-d-1, 0334); BBNP, end of Grapevine Hills Road near Grapevine Springs, 31 May 1990 (Henson & Davis), 1♀ (ASU, D-138, 0514); Mikibbe Springs

off Lost Mine Trail, 23 June 1998 (Henson et al.), 1♀ (ASU, Q-260); Pine Canyon Road, 24 May 1987 (Henson et al.), 1♀ (ASU, A-82); 9 mi S Black Gap on FM 2627, 27 May 1991 (Davis), 1♂ (ASU, J-97, 1582); *Crockett County:* Hwy 195 E Iraan, 18 June 1998 (Henson et al.), 1♂ (ASU, Q-110); *Ector County:* 24 mi W Odessa, 7 June 1979 (Francke & Merickel) 1♂1♀ (WDS); *Hidalgo County:* Edinburg, December 1939 (Mulaik), 2♂1♀ (AMNH); *Jeff Davis County:* Davis Mountain State Park, behind campground, 16 July 1997 (Henson et al.), 1♂ (ASU, P-262); Fort Davis, 8 June 1902 (no collector), 1♀ (AMNH); *Pecos County:* Hwy 285, 12.6 mi N Ranch Road 2401, approx. 37 mi S Stockton roadside picnic area, 6 July 1997 (Henson et al.), 1♀ (ASU, P-75); Ranch Road, 4.2 mi from TX 385, 6 July 1997 (Henson et al.), 2♂2♀ + 2 young (ASU, P-67-70); *Presidio County (Big Bend Ranch State Park):* 3.4 mi W Sauceda (29.28.55N, 104.00.06W), 18 July 1993 (Henson et al.), 1♂ (WTAMU, SC-162); 2.2 mi W Sauceda (29.28.30N, 103.59.17W), 18 July 1993 (Henson et al.), 1♂ (WTAMU, SC-159); 1.1 mi W Sauceda (29.28.42N, 103.58.23W), 13 July 1993 (Henson et al.), 1♂3♀ (WTAMU, SC-134); vicinity of Sauceda (west of bunkhouse, 29.28.01N, 103.57.29W), 17 July 1993 (Henson & Sissom), 1♂ (WTAMU, SC-144); 0.35 mi NE Sauceda (29.28.23N, 103.57.08W), 18 July 1993 (Henson et al.), 2♂1♀ (WTAMU, SC-150,151); 0.9 mi NE Sauceda (29.28.30N, 103.56.38W), 18 July 1993 (Henson et al.), 2♂ (WTAMU, SC-156); 1.45 mi E Sauceda (29.28.25N, 103.56.11W), 11 July 1997 (Sissom), 1♂ (WTAMU, SC-205); FM 170, 1.1 mi W Lajitas (near boundary of park, 29.15.56N, 103.47.24W), 28 May 1997 (McWest & Sissom), 1♀ (WTAMU, SC-183); 7.4 mi inside gate toward Sauceda, 23 June 1999 (Henson et al.), 1♂ (ASU, M-337); 0.35 mi E Sauceda, 18 June 1993 (Henson et al.), 1♂ (ASU, M-116); 0.9 mi E Sauceda, 24 June 1993 (Henson et al.), 4♂ (ASU, M-340, 342, 347, 347A); 0.35 mi E Sauceda, 18 June 1993 (Henson et al.), 2♂ (ASU, M-122, 122A); 0.6 mi from Sauceda, 18 June 1993 (Henson et al.), 1♀ (ASU, M-146); 0.35 mi E Sauceda, 18 June 1993 (Henson et al.), 5♂ (ASU, M-114, 118–121); 6.4 mi from Sauceda, 23 June 1993 (Henson et al.), 1 juv. (ASU, M-323); Jackson Gate, 11 July 1997 (Zrell et al.), 1♂ (ASU, P-254); 1.1 mi from Sauceda, 13 June 1993 (Henson et al.), 1 juv. (ASU, M-21); near Jackson Gate leaving Solitario, 11 July 1997 (Henson et al.), 1♂1♀ (ASU, P-238-239); 0.3 mi from "Y" on east road out of Solitario, 11 July 1997 (Henson et al.), 3♂1♀ (ASU, P-200–203); 2.3 mi E of Big Hill, 5 June 1992 (no collector), 1♂ (ASU, L-340); 0.35 mi E Sauceda, 18 June 1993 (Henson et al.), 4♂1♀ (ASU, M-133, 136–138, 151); bottom of Big Hill, 5 June 1992 (no collector), 1♂ (ASU, L-338); 0.6 mi E gate to BBRSNA, 14 June 1993 (Henson et

al.), 2♂ (ASU, M-69–70); 0.9 mi E Sauceda, 18 June 1993 (Henson et al.), 2♂ (ASU, M-160–161); 0.3 mi E of gate, 14 June 1993 (Henson et al.), 1♂ (ASU, M-55); 1 mi inside gate, 14 June 1993 (Henson et al.), 2♂ (ASU, M-75–76); *Starr County:* FM 755, 2 mi N 83 (rock wall), 19 May 1992 (no collector), 1♂ (ASU, L-74); FM 755, 2 mi N 83, 19 May 1992 (no collector), 7♂1♀ (ASU, L-73, 80, 86, 1784, 1791–1797); Kelsay, hill SE Hwy 83, 24 Dec 1984 (Nilsson), 1♀ (WDS); 5 mi E Rio Grande City, 1 June 1939 (Mulaik), 1♀ + 14 young (AMNH); Rio Grande City, 21 Jan 1939 (Mulaik), 2♂3♀ (AMNH); Rio Grande City, no date (no collector), 1♀ (AMNH); *Terrell County:* Independence Creek/Oak Creek Campground, 7 mi off TX 349, 19 June 1998 (Henson et al.), 1♂ (ASU, Q-114); Independence Creek at SR 349, 26 August 1989 (Van Devender), 1♀ + 4 young (ASU, G-118, 1090); 1 mi S Pecos Co. line (S of Sheffield), 4 June 1986 (Manning), 1♀ (WDS); 19 mi S Sheffield, 16 May 1958 (McAlister), 1♀ (AMNH); 19 mi S Sheffield, 16–17 June 1958 (McAlister), 4♀ (AMNH); Sanderson, 26 May 1952 (Cazier et al.), 1♀ (AMNH); *Tom Green County:* Gun Club Road at 0.1 mi S Convergence in San Angelo (1900', 31.25N, 100.30W, under rock on rocky hillside), 24 May 1993 (McWest), 1♀ (WDS); *Upton County:* 3 mi S, 5 mi E McCarney, 7 June 1986 (Manning), 1♂ (WDS); *Val Verde County:* road to Amsted Recreation Area, E of Pecos River, 22 May 1996 (Henson et al.), 1♀ (ASU, D-2, 0376); 4.8 mi from Hwy 90, 4 July 1997 (Henson et al.), 1♂ (ASU, P-51); Devil's River State Park, under rock near headquarters, 13 May 1996 (Henson et al.), 1♀ (ASU, O-39); Devil's River State Natural Area, by old water tank, 30 June 1997 (Brunner et al.), 1♂ (ASU, P-15); Devil's River, old water tank, 15 June 1999 (Henson et al.), 7♂ (ASU, Q-5–6, 8, 10, 12, 14, 14A); Devil's River State Park, 1 mi from Nature Conservancy line, 17 June 1998 (Henson et al.), 1♂ (ASU, Q-88); Dolan Ranch Nature Conservancy, across river from Devil's River State Natural Area, 17 June 1998 (Henson et al.), 1♀ + 15 young (ASU, Q-67); Devil's River, windmill E of old water tank, 15 June 1999 (Henson et al.), 10♂3♀ (ASU, Q-15, 18, 21–24, 26, 28–33); 5.3 mi N Comstock on TX 1042, under rock outface, 16 May 1996 (Henson et al.), 1♀ (ASU, O-62); Devil's River State Park, across river at Nature Conservancy, 17 June 1998 (Henson et al.), 1♂ (ASU, Q-75); Dolan Ranch W of Devil's River, 2 July 1997 (Henson et al.), 1 juv. (ASU, P-29); Amsted Recreation Area, Pecos River Road to river, 22 May 1990 (Henson et al.), 1♀ (ASU, D-13, 0387); Seminole Canyon State Park, 30 September 1990 (Henson), 1♀ (ASU, F-283); Devil's River State Park, under rock, 13 May 1996 (Baldwin et al.), 1 juv. (ASU, O–38); Devil's River, 13 May 1996 (Henson et al.), 1♀ (ASU, O–40); 1 mi SSE Langtry, 7 June 1974 (Drape et al.), 6♂2♀, 1 juv. (WDS); Langtry, 19 March 1960 (Gertsch et al.), 3♀ (AMNH); *Webb County:* 32 mi E Laredo, 11 Nov 1934 (Mulaik), 5♀ (AMNH); 32 mi E Laredo, 9 Feb 1935 (Mulaik), 1♀ (AMNH); *Zapata County:* off US 83 near Environmental Oil and Gas Company, 12 May 1996 (Henson et al.), 1♂ (ASU, O-32); 2 mi N Zapata (under rock), 16 May 1995 (McWest), 1♂ (WDS). **MEXICO:** *Coahuila:* Saltillo, 22 Aug 1947 (Gertsch), 1♀ (AMNH); *Durango:* Tlahualilo, 1926 (no collector), 2♀ (UAF); *Nuevo León:* El Ebonito, nr. Mouth Sta. Roen w., no date (Pilsbry), 1♀ (ANS); 9 mi NNW, 2 mi N Mina, 15 July 1975 (Liner), 1♀ (FSCA); 10 km E Villa Aldama (steep cliff to north, much lava rock, 1pm), 18 December 1986 (Nilsson), 1♂ (JAN); *Unknown State:* 20 mi E San Pedro, 5 July 1936 (Davis), 1♀ (AMNH).

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LITERATURE CITED

Capes, E.M. 2001. Description of a new species in the *nitidulus* group of the genus *Vaejovis* (Scor-

piones, Vaejovidae). Journal of Arachnology 29: 42–46.

Francke, O.F. 1977. Scorpions of the genus *Diplocentrus* from Oaxaca, Mexico (Scorpionida, Diplocentridae). Journal of Arachnology 2:107–118.

Gertsch, W.J. & M. Soleglad. 1972. Studies of North American scorpions of the genera *Uroctonus* and *Vejovis* (Scorpionida, Vejovidae). Bulletin of the American Museum of Natural History 148:551–608.

Sissom, W.D. 1991a. Systematic studies on the *nitidulus* group of the genus *Vaejovis,* with descriptions of seven new species (Scorpiones, Vaejovidae). Journal of Arachnology 19:4–28.

Sissom, W.D. 1991b. The genus *Vaejovis* in Sonora, Mexico (Scorpiones: Vaejovidae). Insecta Mundi 5:215–225.

Sissom, W.D. 2000. Family Vaejovidae Thorell 1876. *In* Fet, V., W.D. Sissom, G. Lowe, & M. Braunwalder, Catalog of the Scorpions of the World (1758–1998). New York Entomological Society, New York.

Sissom, W.D. & O.F. Francke. 1985. Redescriptions of some poorly known species of the *nitidulus* group of the genus *Vaejovis* (Scorpiones, Vaejovidae). Journal of Arachnology 13:243–266.

Sissom, W.D., G.A. Polis & D.D. Watt. 1990. Field and laboratory methods. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford Univ. Press, Stanford, California.

Sissom, W.D. & S.A. Stockwell. 1991. The genus *Serradigitus* in Sonora, Mexico, with descriptions of four new species (Scorpiones, Vaejovidae). Insecta Mundi 5:197–214.

Soleglad, M.E. 1973. Scorpions of the *mexicanus*

group of the genus *Vejovis.* Wassman Journal of Biology 31:351–372.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. Entomological News 81:297–316.

Stockwell, S.A. 1986. The scorpions of Texas (Arachnida, Scorpiones). Master's Thesis, Texas Tech University–Lubbock. 193 pp.

Vachon, M. 1974. Étude des caractères utilisés pour classer les familles es les genres de Scorpiones (Arachnides). Bulletin du Museum National d'Histoire Naturelle (Paris) (sér. 3) 104: 857–958.

Williams, S.C. 1970a. Scorpion fauna of Baja California, Mexico: Eleven new species of *Vejovis* (Scorpionida: Vejovidae). Proceedings of the California Academy of Science 37:275–331.

Williams, S.C. 1970b. New scorpions belonging to the *Eusthenura* group of *Vejovis* from Baja California, Mexico (Scorpionida, Vejovidae). Proceedings of the California Academy of Science 37:395–418.

Williams, S.C. 1971. New and little known scorpions belonging to the *punctipalpi* group of the genus *Vaejovis* from Baja California, Mexico, and adjacent area (Scorpionida: Vaejovidae). Wassman Journal of Biology 29:37–63.

Williams, S.C. 1980. Scorpions of Baja California, Mexico and adjacent islands. Occasional Papers of the California Academy of Science 135:1–127.

Yahia, N. & W.D. Sissom. 1996. Studies of the systematics and distribution of *Vaejovis bilineatus* Pocock (Vaejovidae). Journal of Arachnology 24:81–88.

THE INFLUENCE OF GROUP SIZE ON DISPERSAL IN THE SOCIAL SPIDER *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

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ABSTRACT. The costs and benefits of group living vary with group size, and competition for resources increases with increasing group size. In the social spider, *Stegodyphus mimosarum,* individuals attain smaller sizes, and survival is lower in larger colonies. In this study we assess whether group size influences the decision to leave a colony—or disperse. Four colony sizes (8, 16, 32 and 64) of *S. mimosarum* were set up under a proportional feeding regime in a laboratory experiment. We expected more spiders to leave large colonies due to intra-group competition. However, there was no significant increase in the number of spiders leaving with increasing group size. Significantly more spiders left a colony during spring and when spiders were larger (at a more advanced stage of development). Variability in access to resources does not promote dispersal, but season and spider size does influence dispersal.

Keywords: Group size, intragroup competition, dispersal, social spiders, *Stegodyphus mimosarum*

The trade-off between the costs and benefits of group living changes with group size (Rannala & Brown 1994; Uetz & Hieber 1997). Social animals interact in groups of sizes that maximize the fitness of the individual (Caraco & Wolf 1975; Sibly 1983; Kramer 1985; Giraldeau & Gillis 1988; Packer & Ruttan 1988; Avilés & Tufino 1998). There is a stable group size, larger than the optimal group size, where the mean inclusive fitness of joining is larger than if the individual remained alone (Sibly 1983; Giraldeau & Gillis 1985; Zemel & Lubin 1995). If the optimal group size cannot be reached, it is preferable for an individual to be in a group larger than optimal rather than a smaller group (Sibly 1983; Giraldeau & Gillis 1985), and most groups in nature are larger than optimal (Sibly 1983; Giraldeau & Gillis 1985; Ward & Enders 1985; Zemel & Lubin 1995). An animal should join a group of supraoptimal size if its fitness would be greater than if it remained alone. Beyond the stable group size, the benefits are too small or the cost levels too high to outweigh the advantages of sociality; and individuals should disperse from this group (Kramer 1985).

In social spiders, there may be advantages to emigration before reproduction or when there is a large increase in numbers in the colony, such as soon after juveniles are born/hatch out, and when the predation effects or parasite loads are too high. In addition, the low genetic diversity in social spider colonies may make dispersal imperative (Smith & Engel 1994). These are the ultimate reasons why animals disperse.

However, the proximate reasons driving the decision to disperse from colonies includes access to resources (Ward 1986), season and size of the animal (Miller & Miller 1991). Resources in a particular area become depleted, and it is advantageous for an animal or a group of animals to find another location before the resources are completely finished. In social animals there may be increased intra-group competition when resources are diminished (Ward 1986).

There are two main aspects to examine with respect to access to resources. First, intra-group competition results in a greater variability in individual access to resources (Ulbrich et al. 1996). In most large social spider nests, competition for resources increased with increasing group size and spiders were less competitive in smaller nests (Ward 1986; Seibt & Wickler 1988a). If the quantity of

prey obtained is proportional to the size of the colony, some individuals may get a higher quantity of food, resulting in a range of individual body sizes within the colony (Ulbrich et al. 1996; Ward 1986). Although the mean mass of spiders is lower in larger colonies, there is no clear indication whether the variance in body mass correlates with colony size (Seibt & Wickler 1988a; Ward 1986). The decision on whether to leave or remain in a group may depend on risk-sensitivity (Uetz 1988). If there is more prey available than the individual needs, remaining in a group reduces the risk of starvation by reducing the variance in the food intake (i.e., foraging in a risk-averse manner). However, when resources are less than the individual requirements (i.e., there is a negative energy budget), it is preferable to move to improve the chance of obtaining resources (i.e., foraging in a risk-prone manner) (Uetz 1988; Lawes & Perrin 1995). This should also apply when there is less access or more competition for food, as is the situation for the disadvantaged spiders in larger nests. Contest competition gives the larger spiders an advantage over the smaller ones (Ulbrich et al. 1996; Ward 1986; Whitehouse & Lubin 1999). Spiders should then leave the larger nests as competition for resources increases, and the smallest spiders should leave.

Second, mean access to resources may also trigger dispersal. The mean food intake per spider decreases with increasing group size, spiders take longer to extract the same amount of food (Ward & Enders 1985) and spiders attain smaller sizes in larger nests (Ward 1986; Seibt & Wickler 1988a, b). Ultimately, competition for resources would have an impact on adult spider size and time of maturity. This should result in spiders dispersing more from larger nests. Dispersal would then be important since it acts as a stabilizing factor by spreading the risk of starvation (Kuno 1980). In addition, in an experiment to test survival rates, more spiders survived from smaller nests than from larger nests (Ward 1986; Seibt & Wickler 1988a). This also suggests that more spiders should leave the larger nests.

We postulated that there would be more intra-group competition in larger colonies. Under conditions of proportional food availability per individual, this would result in a range of individual access to food within each colony with some spiders being disadvantaged. This variability would be greater in larger colonies and the more disadvantaged spiders are expected to leave these colonies.

In this experiment, we tested the influence of variability in the access to resources on dispersal in different colony sizes. We used four group sizes of *S. mimosarum* Pavesi 1883 (Araneae, Eresidae) to test if spiders were more likely to disperse from small groups (low variability in food intake) or large groups (high variability in food intake). We also examined the influence of spider size and the season at which dispersal occurs by conducting the experiment at intervals throughout the year. The influence of mean access to resources will be tested in a subsequent experiment.

METHODS

Twelve nests of *S. mimosarum* were collected from Weenen Nature Reserve, South Africa (28°50′S, 29°51′E) during March 1997, five in June 1997, six in December 1997 and eight from Itala Game Reserve, South Africa (27°31′S, 31°22′E) in April 1998. *Stegodyphus mimosarum* are social spiders, with a life cycle of approximately one year; young spiders emerge from eggs sacs in late summer (February to March) and the adult spiders are found from spring to midsummer (October to January). Data on the growth rate of *S. mimosarum* from Richmond, Kwazulu-Natal is described elsewhere (Crouch & Lubin 2000). Voucher specimens were deposited at the Durban Natural Science Museum.

Nests were maintained in the School of Life and Environmental Sciences, University of Natal, Durban, South Africa under controlled conditions: at 28 °C, on a 12/12 h light/dark cycle to control for seasonal changes in day length. The spiders were fed on a diet of adult mealworms, *Tenebrio molitor,* and mist-sprayed with water once a week. Nests were housed on *Acacia robusta* plants in cages of plastic mesh on a metal frame (1 m diameter × 0.5 m or 1 m high). Each cage had a removable wooden base on a metal stand. The stand could be immersed in water to prevent predation by ants. A tie-up opening at the top of each cage allowed access for feeding.

During preliminary experiments (1996–1997) we found that groups of two and four spiders either did not survive, or did not produce sufficient silk and had difficulty in the

Table 1.—Mean body length and mass of spiders for each of the four trials. Note that the spiders used in the April 1998 trial are closer in size to those used in the October 1997 trial than to those used in the April 1997 trial.

Trial number Month Season	Colony size	Mean body length of colony ± SE (mm)	Mean body length for trial ± SE (mm)	Mean mass (mg)
1 April 1997 Autumn	8	3.44 ± 0.65	3.32 ± 0.08	6.7
	16	3.24 ± 0.79		
	32	3.31 ± 0.94		
	64	3.32 ± 0.72		
2 July 1997 Winter	8	3.96 ± 0.80	3.62 ± 0.34	6.5
	16	3.85 ± 0.70		
	32	3.67 ± 0.71		
	64	3.79 ± 0.59		
3 October 1997 Spring	8	4.55 ± 0.63	4.38 ± 0.17	13.8
	16	4.4 ± 0.71		
	32	4.16 ± 1.01		
	64	4.53 ± 0.93		
4 April 1998 Autumn	8	3.93 ± 1.39	3.97 ± 0.24	12.6
	16	3.71 ± 1.49		
	32	3.94 ± 0.71		
	64	4.29 ± 0.71		

capture and immobilization of adult mealworms. We therefore selected colonies of 8, 16, 32 and 64 spiders for this experiment; to represent small (8), intermediate-sized (16 and 32) and large colonies (64). The selected group sizes of spiders mainly reflected those collected in the field ($\bar{x}$ ± SE = 43.08 ± 31.42, n = 12) although some field nests contained more than 100 spiders.

Spiders removed from nests from both localities (Weenen Nature Reserve and Itala Game Reserve) were randomly allocated into groups to eliminate any source effects. *Stegodyphus mimosarum* individuals from different nests can be combined as they readily accept conspecifics (Seibt & Wickler 1985). At each trial, four replicates of each group size were created, giving a total of 480 spiders in 16 colonies. No spiders were reused in successive trails. The experiment was repeated four times, in April 1997, July 1997, October 1997 and April 1998, to give a range of seasons, spider sizes and levels of maturity. All the spiders used in these trials were immature, i.e., either juvenile or subadult.

The total body length of a sub-sample of spiders was measured from every colony. Every second, third or fourth spider was selected, with a total of 4–14 individuals measured,

depending on the colony size. The average body length was calculated for each colony (Table 1). The mass for each group was measured to four decimal places, on a Mettler AE240 balance, and the average mass of each spider was calculated (Table 1). We preferentially use body length as an indicator of body size (rather than body mass) since it is less affected by the momentary feeding status of the spider. We created a unique color marking for each colony by painting every spider in the colony with two colors of water-based poster paints on the dorsal surface of the abdomen.

Forty-nine *A. robusta* plants (600–700 mm high) were potted in plastic pots (base diameter = 180 mm, top diameter = 240 mm, and height = 205 mm). Each plant was trimmed of all but two or three branches, none of which overhung the pot rim. The plants were arranged in a grid of seven rows, and each row contained seven plants. The pot saucers (outer diameter = 240 mm) were used for the first trial (April 1997), but these were omitted in subsequent trials. The pot centers were 560 mm apart in each row and approximately 820 mm apart diagonally.

The windowless experimental room was artificially lit with 14 "daylight" incandescent

light bulbs of 60 W each, mounted on a metal frame suspended from the ceiling (except for Trial 1, where 8 light bulbs were used on a free-standing frame). The allocation of nests on plants was random. However, no nests were placed on the plants adjacent to the walls, to prevent any edge effect from the proximity of the walls. Each colony was placed on a tree, and enclosed with fine netting, which was tied onto the branch with string. There was sufficient space inside the netting for the spiders to construct a retreat and capture web. Two days later (i.e., Day 0 of the experiment), the netting was removed.

During the experiment, each colony was fed twice weekly—on days 2, 5, 9, 12, 16 and 19 of each trial. Feeding was proportional to the number of spiders in the colony: colonies of eight were fed one prey item per feeding event, colonies of 16 were fed two prey items, colonies of 32 were fed four prey items and colonies of 64 were fed eight prey items.

All movements of spiders were noted daily and each tree or colony was examined for spiders and/or silk. Any spiders within a retreat were left undisturbed, although occasionally the retreat was thin enough to estimate the number of spiders present. Information was recorded on the source of the spiders based on color, the number of spiders and their destinations. The spiders were removed from their new locations each day.

After the first five days, the nests were taken apart, the spiders were counted and the number in each colony was recorded. Spiders that had molted were repainted. Some spiders could not be located and the missing individuals (excluding any dead spiders, since we could not determine the cause of mortality) were replaced so that the original numbers were re-instated. This initial period was termed the Early Trial (1a, 2a, etc.). The colonies were then covered in netting for a further two days, after which the netting was removed. Fourteen days of daily observations then followed. At the end of this period, the nests were again taken apart, all spiders counted and their source noted. This part of the experiment was called Trial 1b, 2b, etc., or the Late Trial. The separate early and late parts of each trial were compared using a Wilcoxon Paired Ranks test, and since no influence of early vs. late trials was found ($Z = -1.903$, $P = 0.056$), the two sections were combined and

averaged. All subsequent analyses were on the combined averaged trials, which increased the internal validity of the data from each colony.

The total number leaving each colony was used to calculate the relative number of spiders that moved (i.e., total number that moved divided by the number in the colony). The data were normalized using an arcsine [square root] transformation and the transformed data were used for all analyses. An analysis of covariance, with a *post-hoc* Bonferroni test, was carried out on each separate section of the experiment (i.e., 1a, 2a, 1b, 2b, etc.). ANCOVA was used to remove the effect of trial date or body size. Arcsine [square root] (relative number moving) was the dependent variable, with colony size (8, 16, 32 and 64) as the factor and trial number or body length as the covariate. The assumptions of the ANCOVA were verified using a Kolmogorov-Smirnoff test to check that the data and residuals were normally distributed, and a Bartlett's Box F-test was used to check for homogeneity of the variances. The assumptions of the parametric tests were met in all cases ($P > 0.05$).

RESULTS

We tested the effect of the mean body size of the spiders on dispersal, for the four trials. The relative number of spiders leaving increased significantly with increasing body length (Linear Regression: $F_{1, 62} = 11.45$, $P = 0.001$) (Fig. 1), and with increasing spider mass (Linear Regression: $F_{1, 62} = 8.21$, $P = 0.006$).

The absolute number of spiders moving increased with increasing colony size (Fig. 2) (ANOVA: $F_{3, 63} = 19.985$, $P < 0.001$). More spiders left the largest colonies (64) compared with the smaller colonies, and this was especially marked during the October 1997 trial. Significantly more spiders left the colonies of 32 in the October 1997 and April 1998 trials compared with the earlier trails. We compared the absolute number of spiders moving with the relative number of spiders moving in each trial (Fig. 3). The relative number of spiders moving increased over the first three trials, ($F_{3, 63} = 8.32$, $P < 0.001$).

We then tested the relative numbers of spiders moving in each colony size. We removed the influence of body length using an AN-COVA, with body length as the covariate (Fig. 4). The trend was for more spiders to leave
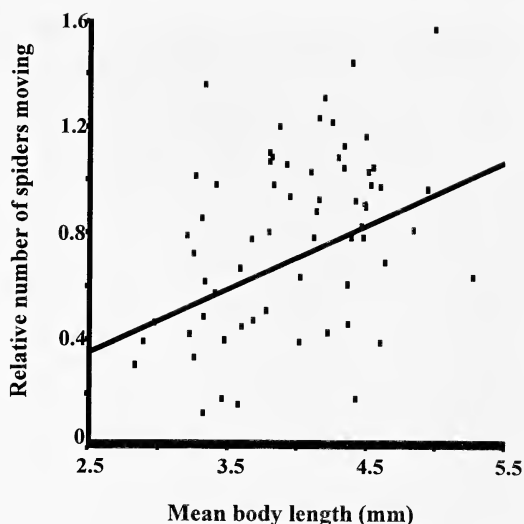
Figure 1.—The influence of body size of spiders on their propensity to move. We plotted the relative number of spiders moving (arcsine square root transformed) against the mean spider body length (mm) for each replicate. The relative number was calculated as the number moving divided by initial colony size.

Figure 2.—The influence of colony size on the propensity to move. The absolute number of spiders moving is plotted against trial. Note that all other analyses presented are on the relative number of spiders moving.

the smaller group sizes, but these results were not statistically significant ($F_{3, 63}$ = 1.34, P = 0.271). Similar results were obtained using spider mass as covariate ($F_{3, 63}$ = 0.82, P = 0.486). We found no influence of colony size on the dispersal of spiders in any of the individual early or late trials or in the combined and averaged early and late trials (in all cases $F_{3, 63}$ < 2.56, P > 0.104). The results for all trials therefore confirm the null hypothesis that group size does not influence dispersal in the group sizes tested.

The numbers of spiders leaving increased over the first three trials with more spiders leaving later in the year (Fig. 2, Fig. 5). Trial date had a statistically significant effect ($F_{3, 63}$ = 11.91, P < 0.001) with significantly more spiders leaving during the October trial than either the April or July trials. The first and fourth trials were both run in the same month of different years, i.e., April 1997 and April 1998. The numbers of spiders leaving during the two April trials are significantly different, with more spiders leaving during the April 1998 trial. Despite this difference, when the two April trials are considered as the same season (autumn), there is still a significant seasonal effect (ANOVA: $F_{2, 63}$ = 6.64, P =

Figure 3.—The influence of colony size on the propensity to move. The effect of mean body length was removed by using the residuals from the regression of the relative number moving (arcsine square root transformed) against spider size. The relative number was calculated as the number moving divided by number in the colony. We plotted the residuals against trial date.
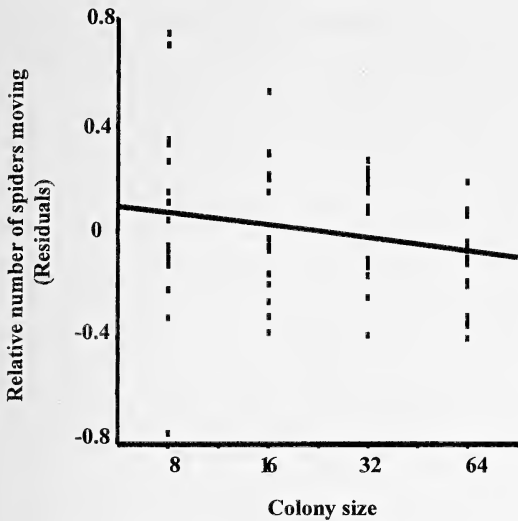
Figure 4.—The influence of colony size on propensity to move. The effect of mean body length was removed by using the residuals of the regression of the relative number moving (actual number moving divided by the number in the colony, arcsine square root transformed) against spider size. We plotted the residuals against colony size. The results were not statistically different ($F_{3, 63}$ = 1.34, P = 0.271). Sample size for each mean = 16 colonies.

Figure 5.—The influence of season on the propensity to move. Variability in spider size was controlled by using the residuals from the regression of the relative number moving (arcsine squareroot transformed) against spider size. We present the mean ± 95% confidence intervals for each trial. Significantly more spiders moved during the spring trial. Note that the two autumn trials are combined (i.e., n = 32 colonies; all others n = 16 colonies).

0.002) with most spiders leaving during the spring (October) trial (Fig. 4). The relative number of spiders leaving for each season was still significantly higher in spring (October) when the effect of body length and mass were removed (ANCOVA: $F_{2, 63}$ = 3.16, P = 0.050; body length and mass as covariate).

We tested the combined effect of colony size and season on the number of spiders moving, in a two-way interaction between the mean number of spiders emigrating in the different colony sizes, with season. We used body length as covariate to remove the effect of body length. We found that there was a significant difference in the effect of mean spider size on the relative number of spiders moving in each trial (Fig. 6). In the April 1997 trial, the number of spiders leaving increased with increasing spider size, while this trend reversed in the subsequent trials despite the larger mean size of the spiders in the later trials. There was a significant interaction effect on the mean number of spiders moving (ANOVA: interaction of colony size and trial:

$F_{9, 63}$ = 2.887, P = 0.008, body length as covariate).

The size of the colony alone did not influence dispersal but there was a combined effect of colony size and season. The dispersing spiders were found on other plants, the walls, ceilings and corners of the experimental room. Most spiders moved during October (spring). Although relative movement from colonies increased with increasing spider size, the mean number moving in each of the later trials decreased.

DISCUSSION

In most large social spider nests, spider size decreases with increasing group size (Ward 1986; Seibt & Wickler 1988a, b). Under conditions of a proportional food supply, intragroup competition results in variability in the individuals' access to resources. We expected this variability to be greater in larger colonies. This should result in relatively more spiders leaving the larger colonies since ultimately such competition would impact on spider size and time of maturity. We found that spider group size alone did not influence dispersal in the group sizes tested.

Other components of fitness (e.g., related-
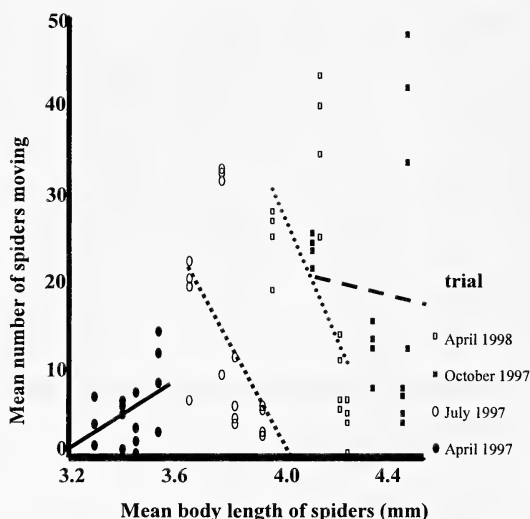
Figure 6.—The influence of the mean size of spiders and the time of year on their propensity to move. We plot the mean number of spiders moving against the mean body length for each colony size in each of the four trials. Note the increasing trend in the number of spiders moving with increasing spider size in the April 1997 trial and the decreasing trend in subsequent trials.

ness of kin) may make it acceptable to have a larger than optimal group size (Rannala & Brown 1994). Very small spiders would not survive outside the nest (Ward 1986). Even with increased competition, it may benefit an individual to stay in a larger nest since variance in body weight may be less in larger colonies (Seibt & Wickler 1988a; Ward 1986). Fitness losses are greater on splitting into groups that are smaller than optimal than they are for remaining in a group that is larger than optimal (Giraldeau & Gillis 1985). Dispersal would only replace intra-group competition with inter-group competition (Zemel & Lubin 1995). The costs of dispersal may also discourage spiders from moving (Aviles & Tufino 1998).

An abundance of insects should be available after the spring rains have fallen and when the trees, on which the spider nests occur, are in flower. Most spiders dispersed during the October (spring) trial, which represents the time when insects would be abundant.

The number of spiders moving increased consistently over the year, with increasing spider size. The influence of body size is most

important in the October 1997 and April 1998 trials. Spiders mature from October onwards and dispersal may be influenced by the sexual maturity associated with the larger size. Burrowing wolf spiders dispersed during spring and autumn and the size of the dispersing spiders determined their survival (Miller & Miller 1991). Field observations on *S. mimosarum* showed dispersal by mature males and females during midsummer (Crouch et al. 1998). Also, dispersal of *Anelosimus eximius* Simon, 1891 (Araneae, Theridiidae) occurs only in inseminated adult females (Vollrath 1982) and *S. mimosarum* adults occur from October through February. Our results show increased dispersal in spring (October), when spiders are larger and adults occur. The larger size of spiders in the April 1998 trial may be attributed to spiders that were laboratory raised for a few months prior to the experiment and hence larger than those in the field at this time.

Although there was an overall increase in the number of spiders moving with increasing spider size, in the later trials this trend reversed. It appears then that for *S. mimosarum,* the influence of spider body size, level of maturity and the time of year (season) with its particular set of environmental conditions, is more important than variability in the access to resources in driving dispersal.

The mean amount of food obtained by each spider is less in larger nests (Ward 1986; Seibt & Wickler 1988a). This would influence adult spider size and ultimately, reproduction. It is then preferable to move to improve the chance of obtaining resources (i.e., foraging in a risk-prone manner) if the amount of food obtained is less than the mean requirements (Uetz 1988; Lawes & Perrin 1995). We are presently testing the influence of mean access to food on dispersal in colonies of *S. mimosarum,* by comparing colonies that have been adequately fed with those that have not been fed.

ACKNOWLEDGMENTS

LITERATURE CITED

Avilés, L. & P. Tufino. 1998. Colony size and individual fitness in the social spider, *Anelosimus eximius.* American Naturalist 152:403–418.

Caraco, T. & L.L. Wolf. 1975. Ecological determinants of group sizes of foraging lions. American Naturalist 109:343–352.

Crouch, T., Y. Lubin & M. Bodasing. 1998. Dispersal in the social spider *Stegodyphus mimosarum* Pavesi, 1883 (Araneae: Eresidae). Durban Museum Novitates 23:52–55.

Crouch, T. & Y.D. Lubin. 2000. Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae) Journal of Arachnology 28:158–168.

Giraldeau, L. & D. Gillis. 1985. Optimal group size can be stable. A reply to Sibly. Animal Behaviour 33:666–667.

Giraldeau, L. & D. Gillis. 1988. Do lions hunt in group sizes that maximize hunters' daily food returns? Animal Behaviour 36:611–613.

Kramer, D.L. 1985. Are colonies supraoptimal groups? Animal Behaviour 33:1031–1032.

Kuno, E. 1980. Dispersal and persistence of populations in unstable habitats. A theoretical note. Oecologia 49:123–126.

Lawes, M.J. & M.R. Perrin. 1995. Risk-sensitive foraging behaviour of the round eared elephant shrew (*Macroscelides proboscideus*). Behavorial Ecology & Sociobiology 37:31–37.

Miller, P.R. & G.I. Miller. 1991. Dispersal and survivorship in a population of *Geolycosa turricola* (Araneae, Lycosidae). Journal of Arachnology 19:49–54.

Packer, C. & L. Ruttan. 1988. The evolution of cooperative hunting. American Naturalist 132:159–198.

Rannala, B.H. & C.R. Brown. 1994. Relatedness and conflict over optimal group size. TREE 9:117–119.

Sibly, R.M. 1983. Optimal group size is unstable. Animal Behaviour 31:947–948.

Seibt, U. & W. Wickler. 1985. Gerontophagy versus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. Animal Behaviour 35:1903–1905.

Seibt, U. & W. Wickler. 1988a. Bionomics and social structure of "family spiders" of the genus *Stegodyphus,* with special reference to the African species, *S. dumicola* and *S. mimosarum.* Verhandlungen des Naturwissenschaftlichen vereins in Hamburg 30:255–303.

Seibt, U. & W. Wickler. 1988b. Why do "Family spiders," *Stegodyphus* (Eresidae), live in colonies? Journal of Arachnology 16:193–198.

Smith, D.R. & M.S. Engel. 1994. Population structure in an Indian cooperative spider, *Stegodyphus sarasinorum* Karsch (Eresidae). Journal of Arachnology 22:108–113.

Uetz, G.W. 1988. Risk sensitivity and foraging in colonial spiders. Pp. 353–377, *In* The Ecology of Social Behaviour (C.N. Slobodchikoff, ed.). Academic Press, London.

Uetz, G.W. & C.S. Hieber. 1997. Colonial web-building spiders: Balancing the costs and benefits of group living. Pp. 458–475, *In* The Evolution of Social Behaviour in Insects and Arachnids (J.C. Choe & B.J. Crespi, eds.) Cambridge Univ. Press, Cambridge.

Ulbrich, K., J.R. Henschel, F. Jeltsch & C. Wissel. 1996. Modelling individual variability in a social spider colony in relation to food abundance and its allocation. Proceedings of the International Congress of Arachnology, Revue Suisse de Zoologie. Vol. hors Serie 13:661–670.

Vollrath, F. 1982. Colony foundation in a social spider. Zeitschrift fur Tierpsychologie 60:313–324.

Ward, P.I. 1986. Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum.* Behaviour 97:213–225.

Ward, P.I. & M.M. Enders. 1985. Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum.* Behaviour 94:167–182.

Whitehouse, M.E.A. & Y. Lubin. 1999. Competitive foraging in the social spider *Stegodyphus mimosarum.* Animal Behaviour 58:677–688.

Zemel, A. & Y. Lubin. 1995. Inter-group competition and stable group sizes. Animal Behaviour 50:485–488.

SEXUAL SIZE DIMORPHISM AND JUVENILE GROWTH RATE IN *LINYPHIA TRIANGULARIS* (LINYPHIIDAE, ARANEAE)

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ABSTRACT.   On three separate occasions during the growth season four populations of the sheet web spider *Linyphia triangularis* were sampled, twice as immatures and once as adults. For the immature specimens, five linear size characteristics (length and width of the cephalothorax, length of tibia of the first leg, and length and height of the abdomen) were measured in the laboratory and compared with fresh weight. The best predictor of weight was abdomen length, closely followed by cephalothorax width. Cephalothorax width was used to compare the size of immatures with the adult size at time of maturity because the abdomen shrinks in the non-foraging adult males. Mean cephalothorax width was larger for males than for females in both immature and adult specimens. The difference increased from the earliest immature population samples to the adult samples. The relationship between cephalothorax width and abdomen length was linear and equal between the sexes over all immature samples. This means that there was no difference in the allocation of resources to body parts important to female fecundity (the abdomen) *vs.* body parts important to male fighting ability (the cephalothorax) between males and females. Selection for large male size thus seems to be greater than selection for large female size in this web-building spider, resulting in an overall faster growth rate in males. Males grow >10% larger than females despite the distinct protandry in this species.

Keywords: Sexual dimorphism, *Linyphia triangularis*, growth rate, spider

Web-building spiders have normally a sexual size dimorphism (SSD) with the female as the larger sex (Vollrath & Parker 1992; Head 1995; Foelix 1996; Coddington et al. 1997). This has been attributed to (1) the development of dwarf males, favored by a high selective adult mortality on males that relaxes sexual selection for large size (Vollrath & Parker 1992), and to (2) the development of giant females (Coddington et al. 1997) in response to fecundity selection for large females as suggested already by Darwin (Andersson 1994).

Both these views support the idea that natural selection favors larger size in female spiders because fecundity is positively correlated with female size in spiders, both intraspecifically (Rubenstein 1987; Suter 1990; Beck & Connor 1992; Higgins 1992) and interspecifically (Eberhard 1979; Marshall & Gittleman 1994; Simpson 1995). Females, which experience a constant and relatively low mortality risk throughout their lives, should grow large to maximize fecundity and reproductive success (Marshall & Gittleman 1994; Head 1995).

Males of web-building spiders run a similar mortality risk as females during juvenile stages, but after maturation they leave their protective web and move around in the vegetation searching for females. This behavior is probably associated with a high risk of mortality (Vollrath 1980), as moving around makes the male more vulnerable to predators and reduces energy reserves. Small size could give an advantage in avoiding visual predators (Gunnarsson 1998); and, because metabolism is lower for small spiders, more time can be used for reproductive activities (Reiss 1989; Blanckenhorn et al. 1995).

Linyphiid spiders exhibit all of the characters of other web-builders, except in regard to size dimorphism, where both sexes are of almost equal size (Vollrath & Parker 1992; Head 1995; Prenter et al. 1997). This probably depends on a more intense sexual selection for large male size through male-male competition over mating opportunities. Protandric mating systems seem to be the rule in linyphiid spiders (Toft 1989; Gunnarsson & Johnsson 1990; Watson 1990), probably because the first male has precedence in fertilization success (Austad 1982; Watson 1991). Males that wait too long for their final molt

risk losing valuable mating opportunities because females reaching sexual maturity mate with the male present in their web. This means that the male growth period is shorter and, assuming an equal growth rate, adult males are expected to be smaller than adult females at maturity.

One linyphiid spider that lives on spruce branches and has a bi-annual life cycle, *Pityohyphantes phrygianus* (C.L. Koch 1836) has been shown to have a male-biased SSD (Gunnarsson 1988). Gunnarsson suggests that this depends on behavioral differences between sexes during winter when males, despite high risk of predation, forage more actively than females (Gunnarsson 1998).

The species used in this study, *Linyphia triangularis* (Clerck 1757), is univoltine and inhabits low shrubs and bushes in many types of habitats in the southern part of Sweden. *Linyphia triangularis* overwinters as eggs, hatches in late March/early April, and grows to adult stage in about four months. Males molt to maturity about a week before females (Toft 1989; Stumpf 1990), and in southwestern Sweden the first adults are seen at the end of July. The adult males guard subadult females, fighting with other males over access to the female, and mate with the female immediately after maturation (Rovner 1968; Nielsen & Toft 1990), leaving mating plugs in the epigynum that impedes further copulation and/or reduce female receptivity (Stumpf 1990; Stumpf & Linsenmair 1995). These studies say nothing about a size dimorphism in either direction, but emphasize the fierce male fights that occur on the web of virgin females, presumably creating a strong sexual selection for large male size. This study was initiated to test whether sexual selection for large male size could overcome fecundity selection for large female size in a linyphiid spider with a continuous growth period. I used four separate populations to control for local variation in size or size dimorphism between populations.

METHODS

Four populations of *Linyphia triangularis* in southwestern Sweden were sampled to control for possible geographic or habitat variation. The NW site (Göteborg) and SW site (Halmstad) were within 5 km from the Swedish west coast, whereas the NE site (Skövde)

and SE site (Värnamo) were inland sites. The SW site was a sparse pine forest, *Pinus sylvestris*, with mostly *Vaccinium myrtillus* as ground cover. The NW site was dominated by heather, *Calluna vulgaris*, with some junipers, *Juniperus communis*, as the only higher vegetation. The SE site is a pine forest, *Pinus sylvestris*, with mixed patches of *Vaccinium uliginosum* and *V. myrtillus* as ground cover. The NW site is on the edge of a mire, with scattered small (< 5 m) birches, *Betula* sp., and pines, *Pinus sylvestris*, as the only higher vegetation, and a ground cover of *Calluna vulgaris*, *Erica tetralix* and *Empetrum nigrum*. The shortest distance between two sites was about 100 km (SW-SE) and the longest distance was about 200 km (SW-NE).

The spiders were collected on three separate occasions from each site between 2 June–5 September 1996. The first sampling was planned to occur about four weeks before the expected maturation but, due to bad weather conditions, the sampling was delayed at two locations. The second sampling was done close to the expected maturation date, and the last sampling was made when the reproductive period was over. To ensure that all spiders had put up new webs, sampling was done only after at least 24 hours of relatively still, clear weather. On each occasion, at least 30 specimens were collected by "hand-to-jar" sampling at random co-ordinates in a selected area of about 10,000 m² with relative homogeneous vegetation. The spiders were brought to the laboratory and placed in darkness at 4 °C overnight before measuring.

On all non-adults I measured the length of the tibia on the first leg, the length (from clypeus to pedicel) and maximum width of the cephalothorax, and the length and height of the abdomen to the nearest 0.02 mm with an ocular eye piece on a Wild stereo-microscope. The fresh weight of the spiders was measured using a Sartorius electronic balance to the nearest 0.1 mg. To control the sex of each individual, the spiders were placed in 250 ml plastic jars and reared to maturity. Spiders that could not be unambiguously sexed before they died were excluded. In adults, most males had shrunken and severely distorted abdomens so only the cephalothoracic measurements were noted in these specimens. Statistical analyses were performed with StatView v.5.0 (SAS In-

Table 1.—Regression statistics of $\log^{10}$ weight against the different $\log^{10}$ linear measurements of body size in juvenile stages. Data from all sites are pooled.

Measurement (x)	Least squares regression on weight (y)	r^2
Cephalothorax length	y = 0.095 + 2.833 x	0.861
Cephalothorax width	y = 0.464 + 3.307 x	0.928
Tibia 1 length	y = 0.080 + 1.963 x	0.714
Abdominal length	y = −0.212 + 2.689 x	0.958
Abdominal height	y = 0.349 + 1.939 x	0.738

stitute 1998) and SuperAnova v.1.11 for Macintosh (Abacus Concepts 1989).

RESULTS

I considered weight as the measure best reflecting the general size of the animals. However, the contrasting adult lifestyles of males and females make the use of adult weight difficult to accurately assess the actual size at maturity. In order to establish the linear measurement that provided the best estimate of general size in *L. triangularis*, I made a logarithmic regression of five linear measurements against the weight of immature spiders. The adults were not used for this test as the

adult male specimens were more-or-less starved and had severely shrunken abdomens. The correlation was high for all the measures in juveniles (Table 1), but the best predictor of weight in the juvenile specimens was abdomen length, closely followed by cephalothorax width. I chose cephalothorax width as indicator of general size instead of weight or other size measurements including the abdomen because this study focuses on the comparison between SSD in juveniles and adults. The deterioration of the males' abdomen during their non-feeding, mate-searching adult life inhibits the use of weight or abdomen length for this purpose.

In order to examine if there was any difference between males and females in allocation of resources to different body parts, i.e., if the relative size of the cephalothorax *vs.* the abdomen changed during growth, I performed a one factorial ANCOVA on abdomen length with sex as factor and cephalothorax width as covariate. Males and females had very similar expected abdomen length for any given cephalothorax width and the only significant factor in the analysis is the covariate, cephalothorax width ($F = 934, 3$; $P < 0.0001$). Neither the interaction term, sex*cephalothorax width ($F = 0, 029$; $P = 0, 86$), nor the singular factor, sex ($F = 0, 007$; $P = 0, 93$), had any effect on abdomen length. The regression lines describing the relationship between maximum cephalothorax width and abdomen length are virtually the same for males and females (Fig. 1). This means that there is no difference between males and females in the relative growth rate of different body parts in juvenile stages.

Males were, on average, larger than females in maximum cephalothorax width in all samples except in the second sample at site SE. In the first sampling at the four sites, males were on average 9–14% larger than females.
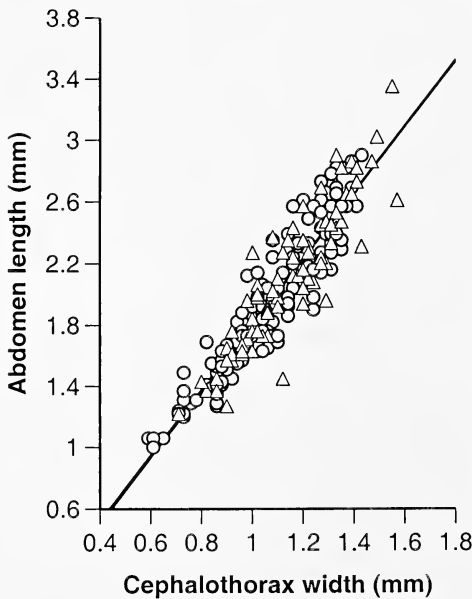
Figure 1.—The relationship between cephalothorax width and abdomen length in immature *Linyphia triangularis*. ○ = females, △ = males. Regressions are: female abdomen length = −0.37 + 2.18 × cephalothorax width, $r^2 = 0.84$; male abdomen length = −0.36 + 2.16 × cephalothorax width, $r^2 = 0.80$.
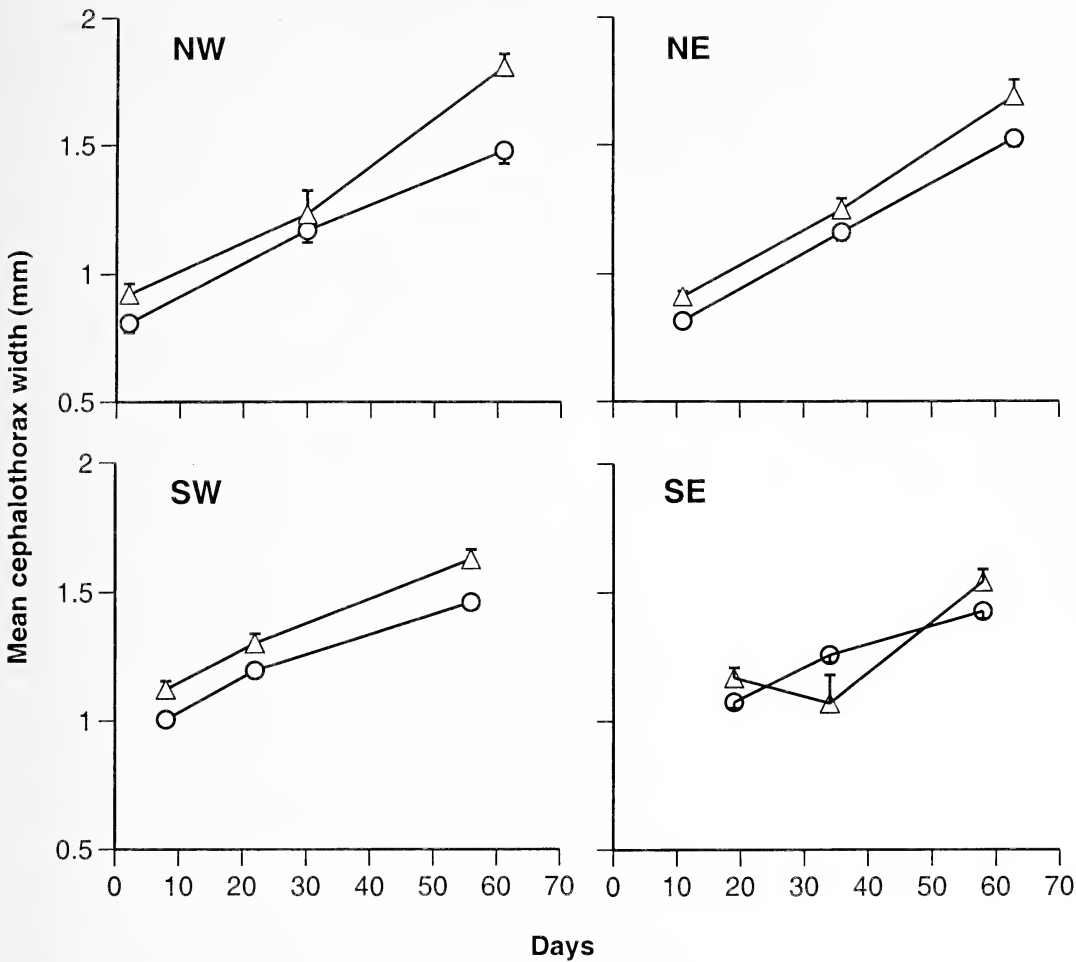
Figure 2.—Development of mean cephalothorax width ± S.E.M. in four populations of *Linyphia triangularis* in SW Sweden. The first sampling yielded only immatures. In the second sampling adults found in the populations were excluded and in the third sampling only adults were found. NW, NE, SW, SE = population labels after relative geographic position. Day 1 = July 1. ○ = females, △ = males.

Mean male cephalothorax width ranged from 0.91 mm in the NE site to 1.17 mm in the SE site, while female mean cephalothorax width ranged from 0.81 mm in the NW site to 1.07 mm in the SE site (Fig. 2). Male abdomen length was on average 12–17% larger than female abdomen length in the four sites.

In the second sampling, made just before the expected molt to maturity, the mean cephalothorax width of males was on average 5–9% larger than that of females in three sites. In the fourth site (SE), few subadult males were found ($n = 2$); and they were much smaller than the subadult females. Male cephalothorax width at this occasion ranged from 1.07 mm in the SE site to 1.30 mm in the SW

site, while female cephalothorax width ranged from 1.16 mm in the NE site to 1.26 mm in the SE site (Fig. 2). The abdomen length varied in a similar way, the males being 7–13% larger than females at three sites, but 28% smaller at the SE site.

The third sampling was made about three weeks after the normal time for maturation. The average cephalothorax width of adults was larger for males than for females in all areas (8–22%). The absolute difference of the average maximum cephalothorax between males and females width was larger in all populations compared to the initial collection. Male adult mean cephalothorax width ranged from 1.54 mm in population SE to 1.81 mm

Table 2.—ANCOVA on cephalothorax width with site and sex as factors and date of sampling as a covariate.

Source	df	Sum of squares	Mean square	F-value	P-value
Site	3	1.142	0.381	20.586	≤0.0001
Sex	1	0.94	0.094	5.060	0.025
Date of sampling	1	12.262	12.262	663	≤0.0001
Site × Sex	3	0.009	0.003	0.154	0.93
Site × Date	3	0.504	0.168	9.085	≤0.0001
Sex × Date	1	0.053	0.053	2.865	0.091
Site × Sex × Date	3	0.042	0.014	0.751	0.52
Residual	323	5.971	0.018		

in the NW population, while female adult mean cephalothorax width ranged from 1.43 mm in the SE population to 1.52 mm in the NE population. All population means of female cephalothorax width were lower than those of male cephalothorax width (Fig. 2).

These results were tested for differences in cephalothorax width with a full interaction, two factor ANCOVA with collection day as a covariate, to control for the time differences between dates of collection, and with sex and site as singular factors (Table 2). There was one significant interaction term in the ANCOVA between site and date of collection. The date of collection, as well as the site of origin, also was highly significant as singular factors; but as the interaction term between these two factors was also significant, these factors cannot be considered independently (Sokal & Rohlf 1995). However, the singular factor sex was not involved in any significant interaction terms and had a significant effect on cephalothorax width ($P = 0.0252$). That shows that males on average have a larger cephalothorax width than females across all sites and times examined.

DISCUSSION

The results in this study show that sexual size dimorphism in *L. triangularis* is generally male-biased in all stages and populations surveyed (Fig. 2). Males are larger than females both as juveniles (first sampling, mostly presubadult stages) and as adults despite their earlier maturation. The size difference, measured as cephalothorax width, increases from the juvenile stages sampled in early July to the adult stages sampled in August. This suggests that males reach a greater weight and overall size at maturity than females do. If so,

males have a higher juvenile growth rate than females, as a solution to two apparently opposing selection pressures on male size in this species. First, males need to mature earlier than females. Female *L. triangularis* mate with the male present immediately after molting to maturity (Toft 1989) and first male to mate with the female sires most of the offspring (Stumpf 1995). This gives males a shorter period of time for growth. Second, because of intense male fights for access to unmated females, males also need to become as large as possible to be able to defend or take over subadult females from other males.

The decrease of the SSD in the second sampling (compared to the first) in some of the populations is probably due to the low numbers of subadult males found in the sample, and that these males were probably smaller than the rest of the cohort. This could depend on (1) reproductive success that is increasing with size but decreasing as time of maturity is delayed and (2) the decision to molt to maturity that will be a compromise between optimal size and age. The result of this would be that larger males mature earlier than small males (Stearns 1992) and that a late sample would then necessarily underestimate the average size of subadults.

Sex-related variation in growth rate was previously described by Wiklund et al. (1991) for the butterfly *Pieris napi* L. 1758 in southern Sweden. This butterfly is partially bivoltine with discreet generations and must diapause as pupae during winter. Males are generally larger than females; but the difference varies depending on the season, as does the mechanism by which the size dimorphism is achieved. Overwintering pupae produce a

first generation of adults in the spring. The eggs laid by these adults can either develop directly, producing a second generation of adults the same year, or they can develop slower into diapausing pupae. Wiklund et al. (1991) shows that the growth rate of the time-stressed larvae that develop directly to second generation adults are higher than for those that develop to diapausing pupae. In the directly developing larvae, males achieve a greater size than females through a higher growth rate. In the diapausing individuals males grow larger than females because they have a longer development time. The authors suggest that growth rate must be considered as a life history trait in its own right amenable to evolutionary change and not as a parameter controlled passively by temperature and food availability in the environment.

The male-biased SSD described in this study is unusual among web-building spiders, and has not been described in other members of the family. Earlier works of SSD in spiders have often used only the total body length as measure of general size, and this may in part explain the difference from the pattern found here. Male-biased SSD in cephalothorax size has previously been described in a study on the orbweaver Metellina segmentata (Clerck 1757) by Prenter et al. (1995). They suggested that the size dimorphism found in the adults of this species depends on sex-specific allocation of resources. This hypothesis states that, because eggs are more costly to produce than sperm, the females make a larger investment in reproductive tissues (i.e., the abdomen). Males can therefore transfer more of their energy to other body parts that assist them in finding and guarding females (such as longer walking legs and a larger, more powerful cephalothorax). However, the large reproductive costs for females are the eggs and the yolk associated with the eggs. Even though oocytes are to some extent present at sexual maturity, the largest part of the egg, the yolk, is not added to the oocytes until after copulation (Seitz 1971). Therefore, the costs of reproductive structures that develop before maturity are likely to be similar in males and females and should not have an effect on overall size dimorphism at maturity.

Also, if there was a difference in resource allocation prior to maturity between females and males of L. triangularis, one would ex-

pect a significant interaction term in the ANCOVA on abdomen length and the slope of the correlation between cephalothorax width and abdomen length (Fig. 2) would be steeper for females than for males. Instead, the slopes between size measurements are virtually identical for males and females. The ANCOVA reveals no difference between males and females in growth of different body parts. This suggests that size dimorphism in L. triangularis depends on an overall higher growth rate in males, as opposed to a sex-related allocation of resources between body parts.

In Pityohyphantes phrygianus, Gunnarsson (1988) showed that subadult males were significantly larger than subadult females in both cephalothorax width and abdomen height both before and after winter. A re-analysis of the data shows that the relationship between the two measurements varies considerably between years and time of season, but the changes are similar for males and females within each sample. This suggests that overall growth rate is higher for males in this species as well and that allocation of resources does not differ between sexes. Pityohyphantes phrygianus is biannual and overwinters twice before maturing in the second spring. In spite of the female-biased primary sex ratio (Gunnarsson & Andersson 1992), it seems to be strong selection on large male size. Males grow larger probably because they forage more actively during winter than females. But foraging actively increases risk of predation, and the result is a more female-biased sex ratio after winter (Gunnarsson 1998).

For L. triangularis, which is a species with a continuous growth period from egg to adult, such an explanation is not possible. Nevertheless, an increased growth rate during juvenile stages would also benefit the female fecundity, unless there is some cost invoked by a high growth rate. Costs could be developmental, for example, if a too-large mass increment between molts would make molting difficult, resulting in loss of one or more limbs—or death. Costs could also arise from a risk-prone feeding behavior, such as responding indiscriminately to any vibration in the web as if it were prey. This would increase the chance that prey falling onto the web is caught, but it also increases the risk to become prey to a larger predator. All of these costs should result in a differential mortality of males, affecting the

sex ratio of the adult population, and possibly also increase the variance of male sizes compared to female size variance. From the data in this study, it is not possible to conclude if there are sexual differences in mortality resulting in a skewed sex ratio in the adult population. Toft (1989) noted that there is an even sex ratio in *L. triangularis* just before maturity and concluded that the operational adult sex ratio therefore is male-biased. This suggests that such costs are negligible.

Another explanation for this male-biased size dimorphism in both juvenile and adult populations could be that males get a headstart in life. This could occur either because male eggs hatch earlier than female eggs or because male eggs are larger than female eggs. Some egg sacs produced by females in the laboratory were allowed to hatch, but there was no apparent differentiation in hatching date within egg sacs. Other egg sacs were opened and the diameter of the eggs within each egg sac was measured. There was no deviation from an expected normal distribution of egg size within these egg sacs (unpubl. data). No study on spiders that I am aware of has reported a differential investment in male and female eggs nor a differential hatching time between eggs. Differential investment might also be very unlikely as the fertilization occurs together with oviposition when the yolk of the egg already has been supplied (Foelix 1996). In conclusion, this work shows that males are larger than females at maturity in *L. triangularis* and that this depends on differences in behavior or physiology that affect the growth rate during juvenile stages. This result suggests that, because of competition for mating opportunities, selection for large size in males is stronger than is selection for large size in females. Since there is no evidence on costs of rapid growth in males, this could mean that there is intraspecific competition that affects males and females asymmetrically. It is also possible that female lifetime reproductive success does not increase monotonically with size, hence the optimal body size for a female is lower than the maximum attainable size.

ACKNOWLEDGMENTS

LITERATURE CITED

Abacus Concepts. 1989. Super Anova. Abacus Concepts, Inc., Berkeley, California.

Andersson, M. 1994. Sexual Selection. Princeton Univ. Press. Princeton, New Jersey. 599 pp.

Austad, S.N. 1982. First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). Evolution 36(4):777–785.

Beck, M.W. & E.F. Connor. 1992. Factors affecting the reproductive success of the crab spider *Misumenoides formosipes*: The covariance between juvenile and adult traits. Oecologia (Berlin) 92:287–295.

Blanckenhorn, W.U., R.F. Preziosi & D.J. Fairbairn. 1995. Time and energy constraints and the evolution of sexual size dimorphism - to eat or to mate? Evolutionary Ecology 9:369–381.

Coddington, J.A., G. Hormiga & N. Scharff. 1997. Giant female or dwarf male spiders. Nature 385:687–688.

Eberhard, W.G. 1979. Rates of egg production by tropical spiders in the field. Biotropica 11(4):292–300.

Foelix, R.F. 1996. Biology of Spiders (2nd ed.). Oxford Univ. Press, Oxford. 330 pp.

Gunnarsson, B. 1988. Body size and survival: Implications for an overwintering spider. Oikos 52:274–282.

Gunnarsson, B. 1998. Bird predation as a sex- and size-selective agent of the arboreal spider *Pityohyphantes phrygianus*. Functional Ecology 12:453–458.

Gunnarsson, B. & A. Andersson. 1992. Chromosome variation in embryos of a solitary spider, *Pityohyphantes phrygianus*, with skewed sex ratio. Hereditas 117:85–91.

Gunnarsson, B. & J. Johnsson. 1990. Protandry and moulting to maturity in the spider *Pityohyphantes phrygianus*. Oikos 59:205–212.

Head, G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (Class Araneae). Evolution 49(4):776–781.

Higgins, L.E. 1992. Developmental plasticity and

fecundity in the orb-weaving spider *Nephila clavipes*. Journal of Arachnology 20:94–106.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: Is more better? Functional Ecology 8:118–124.

Nielsen, N. & S. Toft. 1990. Alternative male mating strategies in *Linyphia triangularis* (Araneae, Linyphiidae). Acta Zoologica Fennica 190:293–297.

Prenter, J., W.I. Montgomery & R.W. Elwood. 1995. Multivariate morphometrics and sexual dimorphism in the orb-web spider *Metellina segmentata* (Clerck, 1757) (Araneae, Metidae). Biological Journal of the Linnean Society 55:345–354.

Prenter, J., W.I. Montgomery & R.W. Elwood. 1997. Sexual dimorphism in northern temperate spiders: Implications for the differential mortality model. Journal of Zoology, London 243:341–349.

Reiss, M.J. 1989. The Allometry of Growth and Reproduction. Cambridge Univ. Press, Cambridge. 182 pp.

Rovner, J.S. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). Zeitschrift fuer Tierpsychologie 25:232–242.

Rubenstein, D.I. 1987. Alternative reproductive tactics in the spider *Meta segmentata*. Behavioral Ecology and Sociobiology 20:229–237.

SAS Institute. 1998. StatView, 2nd ed. SAS Institute Inc., Cary, North Carolina.

Seitz, K.-A. 1971. Licht-und elektronenmikroskopische Untersuchungen zur Ovarienentwicklung und Oogenese bei *Cupiennus salei* Keys. (Araneae, Ctenidae). Zeitschrift fuer Morphologie der Tiere 69:283–317.

Simpson, M.R. 1995. Covariation of spider egg and clutch size: The influence of foraging and parental care. Ecology 76(3):795–800.

Sokal, R.R. & F.J. Rohlf. 1995. Biometry (3rd ed.). W.H. Freeman & Co., New York. 887 pp.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford Univ. Press, Oxford. 249 pp.

Stumpf, H. 1990. Observations on the copulation behaviour of the sheet-web spiders *Linyphia hortensis* Sundevall and *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). Bulletin of the Society of European Arachnology 1:340–345.

Stumpf, H. & K.E. Linsenmair. 1995. Observations on the mating systems of two spiders, *Linyphia hortensis* Sund. and *L. triangularis* (Cl.) (Linyphiidae: Araneae). Revue Suisse de Zoologie (vol. hors série) 627–634.

Suter, R.B. 1990. Determinants of fecundity in *Frontinella pyramitela* (Araneae, Linyphiidae). Journal of Arachnology 18:263–269.

Toft, S. 1989. Mate guarding in two *Linyphia* species (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 8(2):33–37.

Vollrath, F. 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. Zeitschrift fuer Tierpsychologie 53:61–78.

Vollrath, F. & G.A. Parker. 1992. Sexual dimorphism and distorted sex ratios in spiders. Nature 360(6400):156–159.

Watson, P.J. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). Behavioral Ecology and Sociobiology 26:77–90.

Watson, P.J. 1991. Multiple paternity and first mate sperm precedence in the sierra dome spider, *Linyphia litigiosa* Keyserling (Linyphiidae). Animal Behaviour 41(1):135–148.

Wiklund, C., S. Nylin & J. Forsberg. 1991. Sex-related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly, *Pieris napi*. Oikos 60:241–250.

PREDATORY BEHAVIOR OF THREE SPECIES
OF SAC SPIDERS ATTACKING CITRUS LEAFMINER

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ABSTRACT. The predatory habit of three species of sac spiders, *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus*, on citrus leafminer, *Phyllocnistis citrella*, was investigated. Observation of spider activities during the photophase and the scotophase confirmed that these three species of sac spiders are nocturnal. They detect their prey by sensing vibrations of the substrate induced by the concealed prey. Movements of *P. citrella* larvae and prepupae appear to create vibrations of the leaf substrate, which then serve as cues for the spiders to locate them. The searching and prey capture behaviors of these spiders are discussed. Two methods of prey attack were exhibited. In one method, the spider punctures the mine, immobilizes the larva and then bites it and sucks the larval body fluid. In the second behavioral pattern, the spider makes a slit in the mine, uses its forelegs to pull the larva or prepupa out of the mine, holds the prey securely, and finally bites it and regurgitates digestive juices into the prey and ingests the pre-digested liquid tissue.

The three species of sac spiders were found to start feeding on *P. citrella* larvae during the 2nd instar stage. Consumption increased as they developed to later instars. Maximum consumption for all species was recorded at the 4th instar. Although *C. inclusum* and *T. volutus* can complete their life cycle with *P. citrella* as their only food, *H. velox* was not able to develop to the adult stage. Results obtained from this study provide useful data to better understand the role of sac spiders in the overall management of *P. citrella*.

Keywords: Nocturnal, prey capture, feeding stage, *Phyllocnistis citrella*, sac spiders

The citrus leafminer, *Phyllocnistis citrella* Stainton (1856) (Lepidoptera, Gracillariidae) has become an important pest of *Citrus* spp. in Florida since its introduction in 1993 (Knapp et al. 1995). The larvae of *P. citrella* mine in leaf tissues of any citrus and related species (Heppner 1993). *Phyllocnistis citrella* larval feeding results in citrus plants with distorted and reduced young shoots. Severe pressure from *P. citrella* causes decrease in yields and quality (Knapp et al. 1995; Heppner 1995; Burgeous & Constantin 1995). Although many insect parasitoids of this pest have been recorded (Heppner 1993), little attention has been directed towards predators of the larvae. Predatory arthropods are believed to make an important contribution to the mortality of *P. citrella* (Zhao 1989; Zhang et al. 1994; Argov & Rossler 1996; Browning & Peña 1995; Amalin et al. 1995; Peña & Subramanian unpubl.). In Israel, spiders were observed in the field to prey upon *P. citrella* (Argov & Ros-

sler 1996). Likewise, in south Florida, various species of spiders were considered important in reducing peak populations of *P. citrella* (Browning & Peña 1995; Amalin et al. 1995). Feeding tests on 14 commonly encountered spider species in lime orchards in Homestead, Florida confirmed that the three species of sac spiders, *Chiracanthium inclusum* (Hentz 1847) (Clubionidae), *Hibana velox* (Becker 1879) (Anyphaenidae), and *Trachelas volutus* Gertsch 1935 (Corrinnidae), fed on *P. citrella* larvae and, in some cases, on prepupae (Amalin 1999). Apparently these species of spiders are able to detect and attack the larvae through the leaf epidermis. This phenomenon of search and extraction of a cryptic food source has not been reported in this group of spiders. Because of this specialized feeding behavior, these spiders may prove to be important predators of *P. citrella*. Study of the predatory habits of these spiders on citrus leafminer is of paramount importance to better
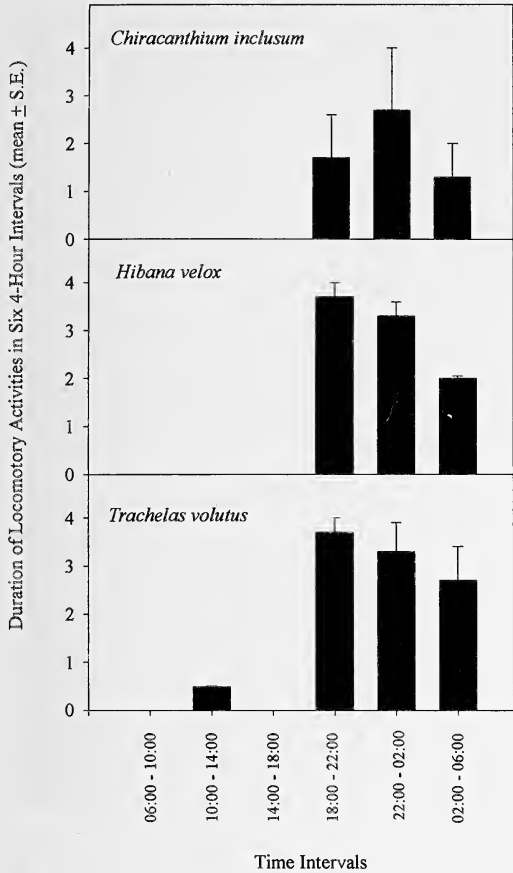
Figure 1.—Duration of locomotory activities in three species of sac spiders measured in six 4-hour intervals. Lights turned off at 1800 h.

understand the potential of these predators as a component of the natural enemy complex of *P. citrella*.

In this paper, investigations of the predatory behavior of three species of sac spiders (*C. inclusum*, *H. velox*, and *T. volutus*) attacking *P. citrella* is reported. The main objectives of this study were to determine the time of feeding activity, to investigate the predation strategy, and to identify the developmental stages of spiders that feed most actively on *P. citrella*.

METHODS

Sources of test organisms.—Egg sacs of *C. inclusum*, *H. velox*, and *T. volutus* were collected from citrus orchards in the vicinity of Homestead, Florida. Egg sacs were identified based on descriptions by Amalin (1999). They were brought to the laboratory and

maintained in the incubator at 27 °C, 80% RH, and 12:12 h photoperiod and reared on an artificial diet (Amalin 1999). Laboratory-reared 4th instar spiders were used for the experiments to determine the time of feeding activity and predatory strategy. *Phyllocnistis citrella* larvae were collected from a culture on lime (*Citrus aurantifolia*) plants maintained in the greenhouse. Voucher specimens are deposited at the Tropical Research and Education Center, Dept. of Entomology, Homestead, Florida.

Time of feeding activity.—Feeding times of the three sac spiders were determined from observations over a 24 hour period. A plastic petri plate (10.5 cm diameter × 2.0 cm high) was used as the observational arena. Lime leaves with five *P. citrella* larvae within the serpentine mines were placed in each petri plate. The number of *P. citrella* exposed to the spider is based on the result of the predation experiment previously conducted (Amalin 1999), in which a ratio of one spider to 10 *P. citrella* larvae gave an average of 5.3 *P. citrella* larvae consumed.

A single 4th instar spider was placed in each arena that was lined at the bottom with moistened filter paper to retain the freshness of the leaves. The test spiders were fed with artificial diet (Amalin et al. unpubl.) for 24 h before transferring to each petri plate; in this way the hunger level is controlled. All the petri plates were placed in an incubator with constant temperature (27 °C), relative humidity (80%), and a 12:12 h photoperiod. These were the same conditions under which spiders have been previously reared. Observations of spider activities were made every 15 min during the photophase and during scotophase by the use of a portable red light with an intensity of 5.0 Lux. Some arthropods (Borror et al. 1992; Jackson 1977) cannot recognize red light. Thus, red light is used to observe their nocturnal activities. The set-up was repeated three times on separate dates for each of the three spider species. The circadian rhythm of locomotory activity was observed to determine if they are diurnally or nocturnally active animals. Duration of movement in six 4 h intervals (0600–1000, 1000–1400, 1400–1800, 1800–2200, 2200–0200, 0200–0600) was noted.

Predatory strategy.—Spider activities were recorded by videotaping, using a video
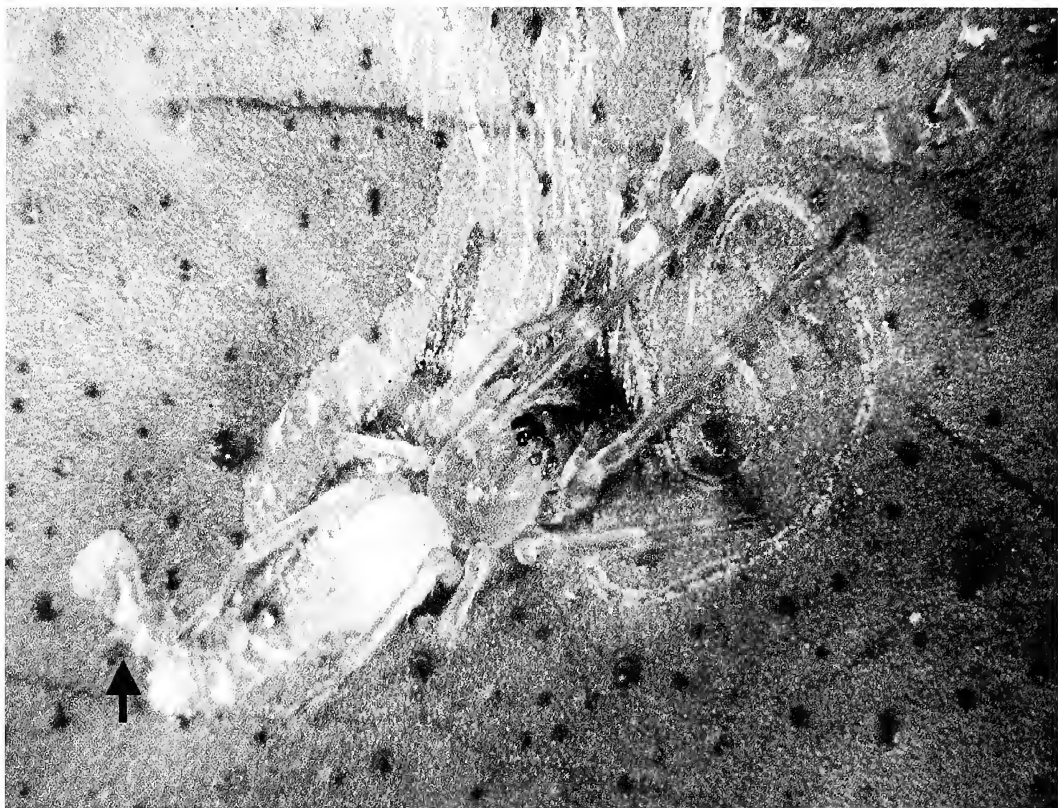
Figure 2.—*Chiracanthium inclusum* touching or sensing the *Phyllocnistis citrella* larva by its hindleg. Arrow shows the *P. citrella* larva still within the serpentine mine.

time lapse cassette recorder (Panasonic Model AG-6730). A television monitor (Sony Trinitron) and a video camera (Javelin Chromachip V, Model JE-3662RGB) were hooked-up to the video recorder. The video camera was held on top of a tripod. The three species of sac spiders included in this observation were placed separately in a small petri plate (3.5 cm diameter × 0.5 cm high). The petri plate was provided with five *P. citrella* 2nd instar larvae still within their serpentine mines. The petri plate was positioned under the tripod. The exact position of the petri plate was determined by looking at the television monitor. The video machine was set to 16 h recording continously. The videotaping was conducted in a room with lights off from 1800 h until 0700 h the next day. To have a clear view of the predatory activity under total darkness, red lights (5.0 Lux intensity) were provided under the tripod. The set-up was repeated five times for each species. After videotaping, each tape was viewed and the following data were gath-

ered: retreat period (no locomotion, no body movement, the spider remained inside the retreat nest); searching time (locomotory activity); and handling time (period from start of attack until prey was consumed). The mean and standard error of the time spent for each activity were calculated. The number of *P. citrella* consumed was counted under a microscope the following morning and the average number of *P. citrella* consumed was calculated. The mean difference for each parameter was compared using Duncan Multiple Range Test (DMRT) (SAS 1989).

Active feeding stages.—to determine spider developmental stages capable of feeding on *P. citrella*, the three species of spiders were reared from the 2nd instar to the adult stage using *P. citrella* larvae their sole food source. Ten *P. citrella* 2nd instar larvae within the serpentine mines were placed in each petri plate (10.5 cm diameter × 2.5 cm high). Individual 2nd instar spiders were introduced into each petri plate. Ten spiders of each spe-
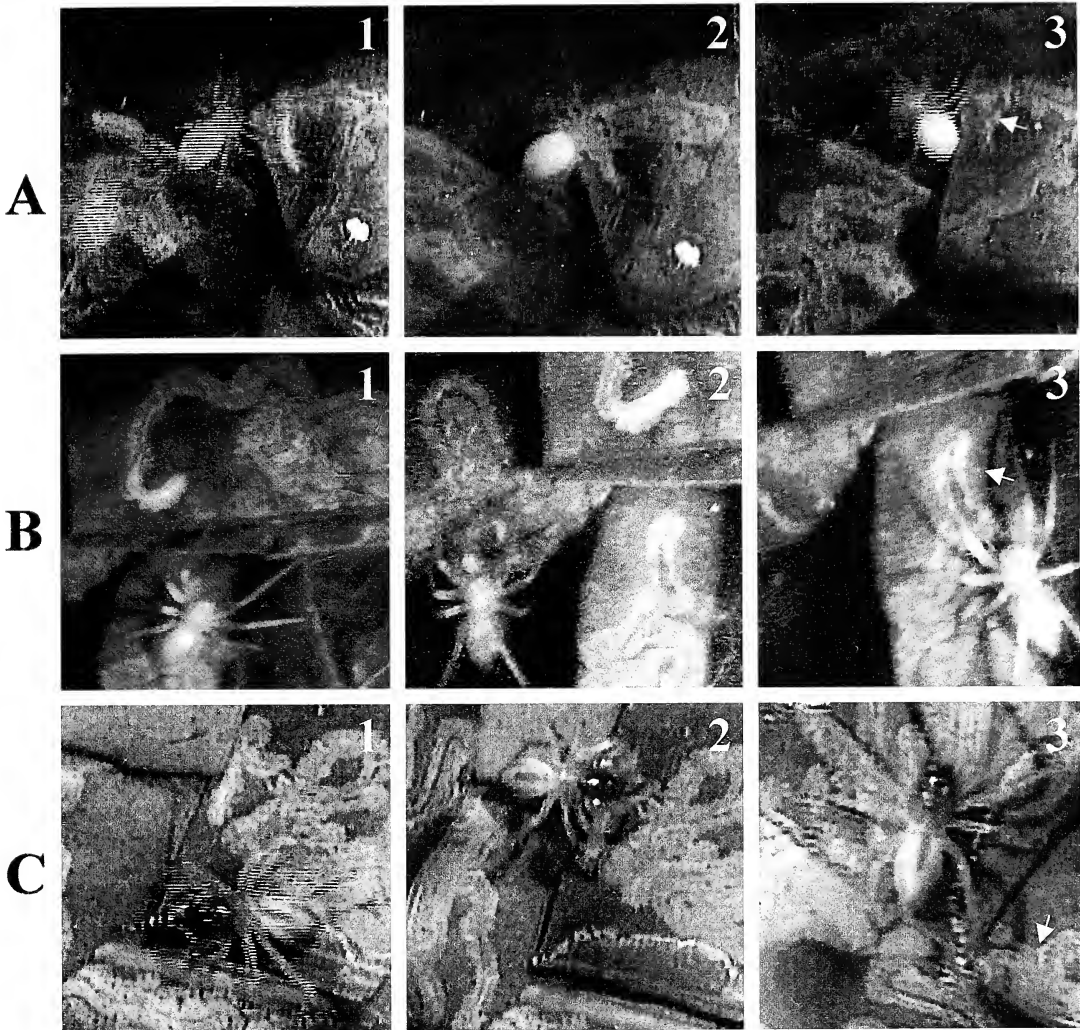
Figure 3.—Predation sequence of (A) *Chiracanthium inclusum,* (B) *Hibana velox,* (C) *Trachelas volutus*—searching (1), feeding (2), and after feeding (3). Arrows in A3, B3, and C3 show the empty serpentine mines after spider feeding.

Table 1.—Duration of time for predation activity and the percent *Phyllocnistis citrella* consumption in 24 hours by the 4th instar spiderlings of *Chiracanthium inclusum, Hibana velox,* and *Trachelas volutus.* All figures are mean ± S.E. of five replications. Means in each column with the same letters are not significantly different according to DMRT.

Spider species	Searching time (min)	Handling time (min)	% *P. citrella* consumption
Chiracanthium inclusum	22.8 ± 7.6 a	10.8 ± 2.5 a	60.0 ± 24.0 b
Hibana velox	8.8 ± 4.8 b	11.3 ± 5.7 a	64.0 ± 16.0 b
Trachelas volutus	5.5 ± 1.2 b	6.5 ± 4.7 a	90.0 ± 11.0 a

Table 2.—Percent *Phyllocnistis citrella* larval consumption by the different instars and adult stage of *Chiracanthium inclusum*, *Hibana velox* and *Trachelas volutus*. All figures are mean ± S.E. of 10 replications. Data for immature stages of female and male spiders for all species are pooled.

| Species | Immature (instar) stage | | | | | | Adult | |
	2nd	3rd	4th	5th	6th	7th	Female	Male
C. inclusum	38.2 ± 4.1	44.8 ± 4.1	57.0 ± 7.0	27.9 ± 7.6	35.6 ± 14.0	8.4 ± 8.4	37.0 ± 15.0	34.3 ± 17.0
H. velox	25.6 ± 3.0	46.2 ± 6.0	70.5 ± 6.5	57.2 ± 11.4				
T. volutus	58.7 ± 9.7	47.2 ± 5.4	61.3 ± 11.8	45.3 ± 14.6			70.7 ± 7.6	65.3 ± 9.6

cies were included in the experiment. Dead *P. citrella* larvae were counted every other day, and after the mortality reading, new citrus leafminer larvae were added to each petri plate to keep the number of *P. citrella* constant. The molting period was recorded for each spider to determine the developmental stages.

RESULTS

Time of feeding activity.—The mean duration of locomotory activity for each species was grouped in six 4 hour time intervals. Our observations confirmed that *C. inclusum*, *H. velox*, and *T. volutus* are all active nocturnally (Fig. 1). The onset of movement for *C. inclusum* and *H. velox* was at the beginning of interval 4, which was about one hour into the scotophase. One out of the three *T. volutus* showed some locomotory activity 4 h into the photophase. The observed daytime activity of this individual *T. volutus* was very brief, lasting only for two consecutive 15 min obervation periods, and was followed by a retreat period of about 7 hours. The peak of locomotory activity for the three species occurred during intervals 4 and 5. The locomotory activity was reduced at the end of interval 6.

Predatory strategy.—The pattern of the prey capture sequence was similar for the three species of sac spiders. During the searching period, the spiders would move about and then stop for a while as if to localize the source of the vibration. Immediately upon touching the prey with its legs (Fig. 2), the spider would turn very rapidly toward the prey and grasp it. Figure 3 shows the predation sequence of these three species of sac spiders. Two behavioral patterns of prey attack were exhibited by the three species of sac spiders. In one strategy, the spider punctured the mine, immobilized the larva, bit it and sucked the larval body fluid (Fig. 3A & C). In the second behavioral pattern, the spider made a slit on the mine, and then used its forelegs to pull the larva or prepupa out of the mine (Fig. 3B). The first gentle touch with the forelegs, probably aided by special sensory hairs on the forelegs, was quickly changed into a powerful grip. Only after the prey has become immobilized by the venom does the spider begins to feed (chew and exude digestive juice).

The searching time or the time to locate the prey differed among the three species. An av-

Figure 4.—Development of (A) female and (B) male *Chiracanthium inclusum* raised using *Phyllocnistis citrella* larvae. Arrows refer to molt when a new instar stage begins.

erage of 5.5, 8.8, and 22.8 minutes was spent on prey location by *T. volutus*, *H. velox*, and *C. inclusum*, respectively (Table 1). It took *C. inclusum* significantly longer time to locate the prey than *T. volutus* and *H. velox*. There was no significant difference in the time spent by the three species of spiders to handle and feed on *P. citrella* (Table 1). Moreover, it was observed that *C. inclusum* and *H. velox* moved more frequently in the observational arena than *T. volutus* did. The postfeeding (resting) period for *C. inclusum* and *H. velox* was extensive, while that of *T. volutus* was brief. These behavioral differences may explain why the average percent *P. citrella* consumption

was significantly higher for *T. volutus* (90%) than for *C. inclusum* (60%) and *H. velox* (64%) (Table 1).

Active feeding stage.—Our observations revealed that *C. inclusum*, *H. velox*, and *T. volutus* started to feed on *P. citrella* larvae as 2nd instar spiders. The percent *P. citrella* consumption for the three species of sac spiders differed among the different instars and adult stage (Table 2). Maximum consumption was recorded at the 4th instar for all species. This stage has progressed midway to the adult stage, and they feed voraciously to meet the energy and nutritional demands of final maturation. *Chiracanthium inclusum* and *T. vol-*
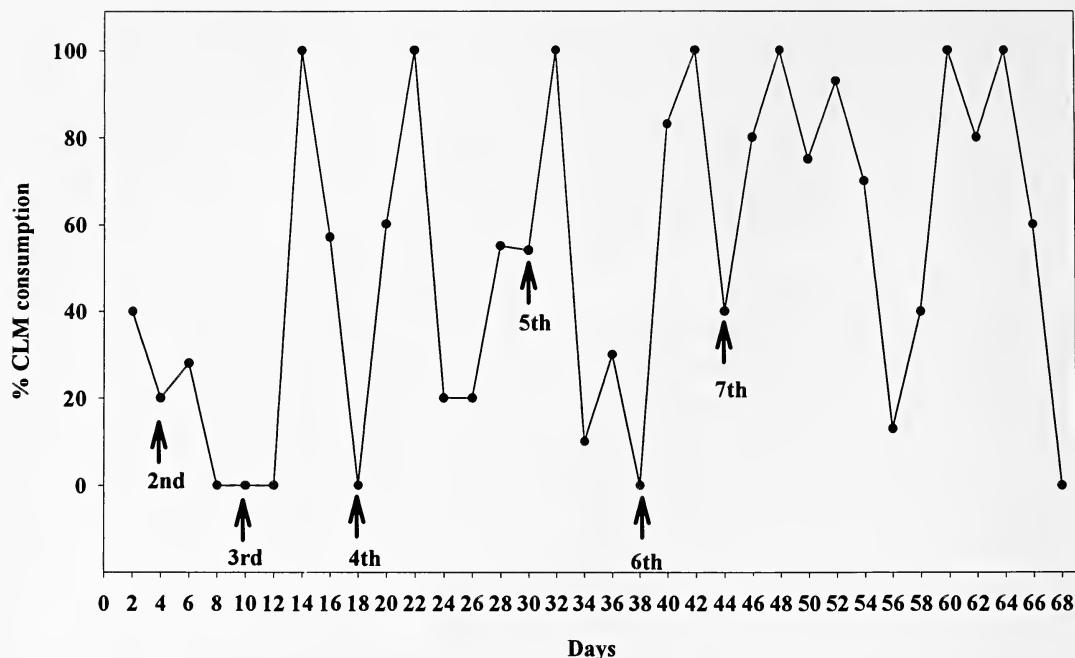
Figure 5.—Development of *Hibana velox* raised using *Phyllocnistis citrella* larvae. Arrows refer to molt when a new instar stage begins. The female and male immature stages are pooled.

utus can complete their life cycles with *P. citrella* as their only food source (Table 2); however, *H. velox* was unable to complete its life cycle by feeding solely on *P. citrella* (Table 2). For all of the species, feeding slowed down and sometimes stopped for 1–2 days before molting and then resumed after the molt. Individual spiders had different time intervals from one molting period to the next. Figures 4–6 show an example of the development pattern of the three species of spiders from the 2nd instar to the adult stage.

DISCUSSION

The 24 hour observation periods revealed that *C. inclusum*, *H. velox*, and *T. volutus* are generally nocturnally active animals. The brief locomotory activity of *T. volutus* during the daytime could mean that *T. volutus* may be also active for short times during the day. This could be verified by doing more daytime observations. The activity of most wandering spiders is correlated with a particular light level (Seyfart 1980). In the field we rarely see these spiders in the daytime unless we venture to look at their retreat nests. These spiders have poor vision. Their eyes are simple (Land 1985); and they rely little, if at all, on visual

cues in prey capture sequences. They possibly detect their prey through vibration of the substrate where the prey is concealed. The constant movement of *P. citrella* larvae while feeding on tissues under the leaf epidermis probably creates the vibrations of the leaf substrate (I. Jackson pers. commun.). It appeared then that such vibrations serve as the cue for the spiders to locate the position of the larva or prepupa of *P. citrella*. The wandering spider *Dolomedes* sp. can distinguish between the ripples caused by the wind and the surface vibrations generated by an insect (Bleckmann & Rovner 1984). This may be true also for *C. inclusum*, *H. velox*, and *T. volutus*. The surface vibration produced by the movement of *P. citrella* larval feeding probably has a characteristic level of frequency and amplitude that can be distinguished by the sac spiders. However, this remains to be verified.

The prey capture sequence exhibited by *C. inclusum*, *H. velox*, and *T. volutus* followed the entire prey capture stages summarized by Foelix (1996) for wandering spiders. For this group of spiders, the main signal for prey capture is mechanical vibration. Once the prey is located, the spider grasps the prey with the
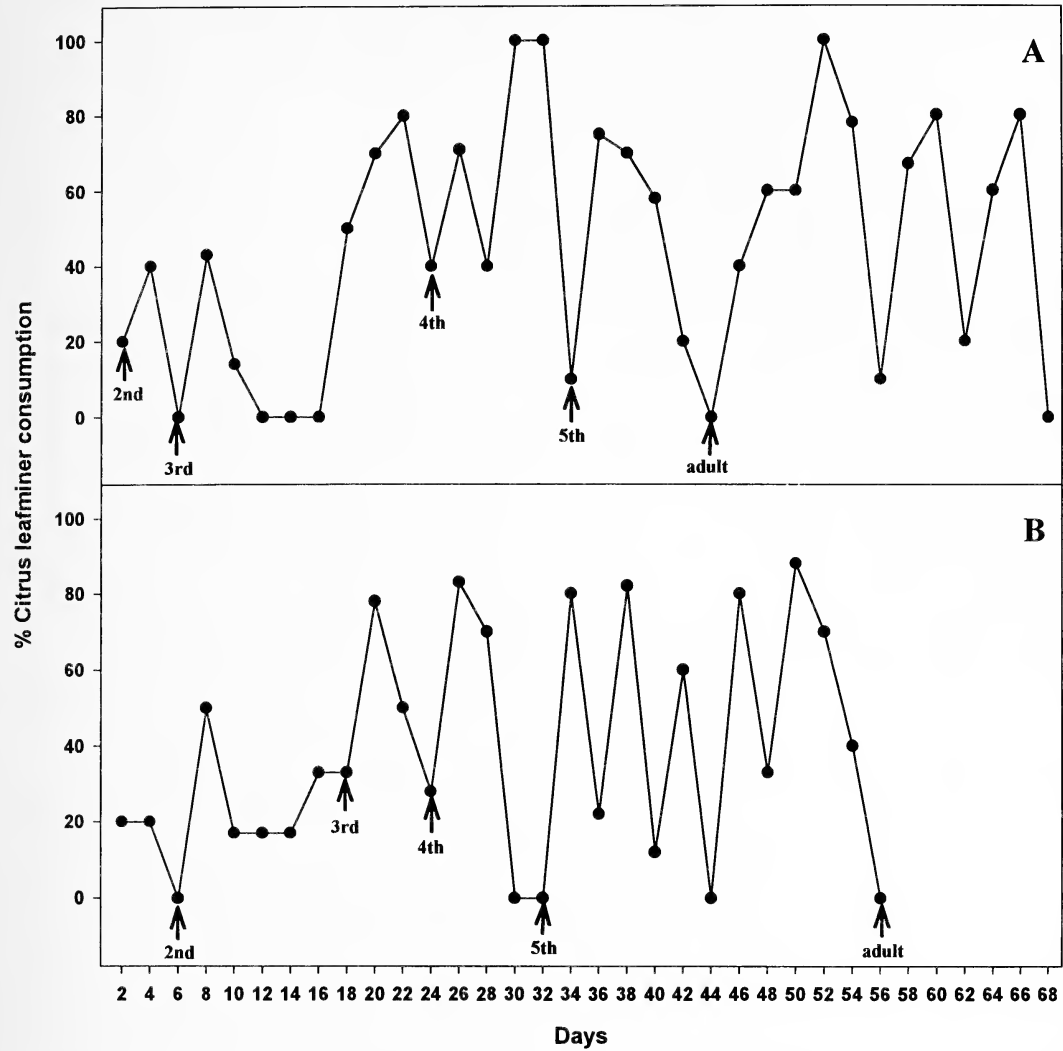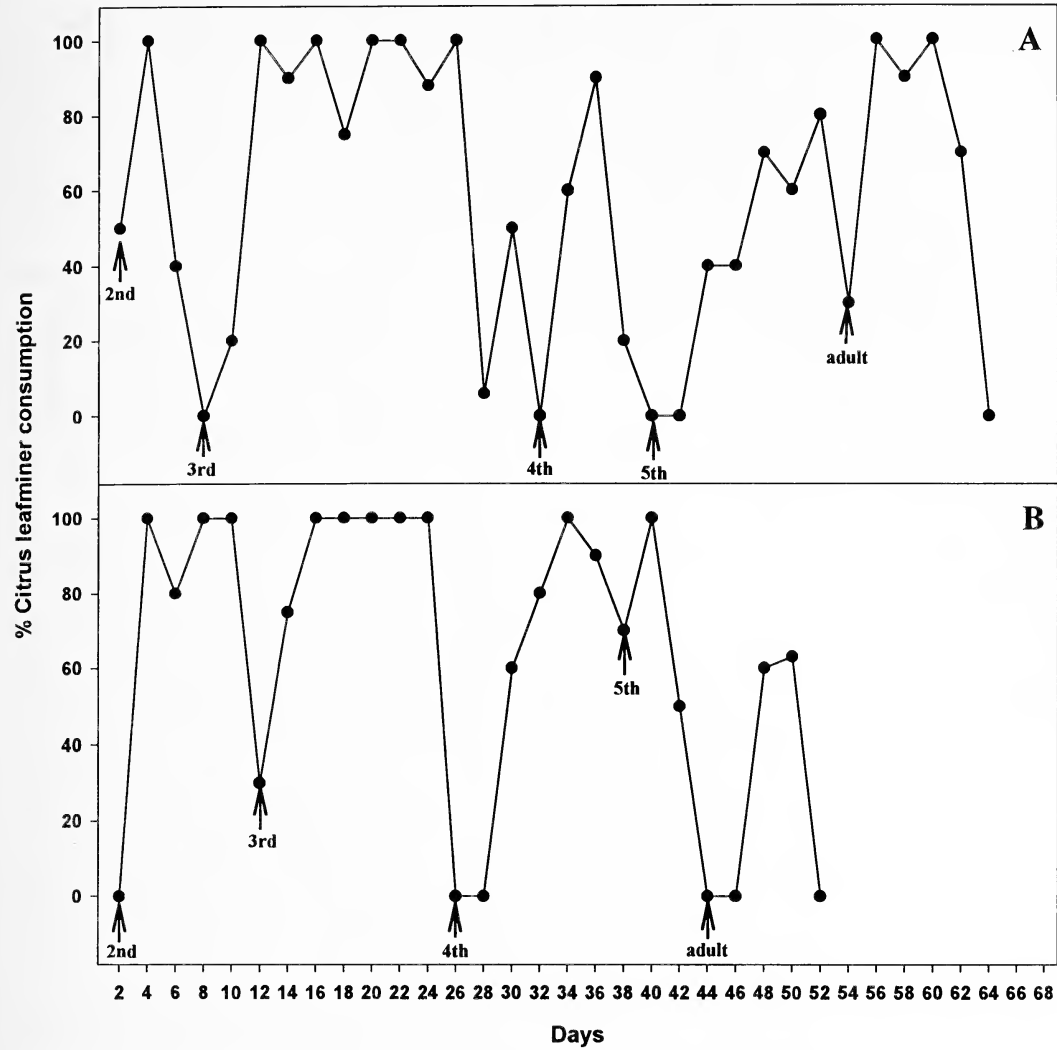
Figure 6.—Development of (A) female and (B) male *Trachelas volutus* raised using *Phyllocnistis citrella* larvae. Arrows refer to molt when a new instar stage begins.

tips of the front legs. Rovner (1978) reported that for the wandering spider *Cupiennius* sp. the forelegs are able to further secure their hold by means of the adhesive hairs or scopulae on the tarsi. This may also be so for *C. inclusum, H. velox,* and *T. volutus* since these three species of sac spiders possess tarsal scopulae and dense claw tufts (Roth 1993; Edwards 1958; Platnick 1974). After the spider secured its hold, the prey was quickly pulled toward the spider's body. Thereupon the chelicerae of the spider's fangs moved apart and were inserted quickly into the nearest part of the victim's body. Immediately after the bite, the tips of the legs released their grip and the

prey was held in the air only with the chelicerae. The behavior appears to minimize any danger to the spider from the prey. Holding the prey aloft is advantageous to the spider because the victim cannot apply any force against the substrate to free itself.

The three species of spiders started to feed on *P. citrella* larvae during their 2nd instar. This is not surprising since spiders, after molting into the 2nd instar stage, are generally found to be self-sufficient (Foelix 1996). At this stage, they have developed their sensory hairs, their legs are equipped with the typical claws, they have bulging eyes, and their mouthparts are already differentiated suffi-

ciently for capturing and feeding on prey. Then, the consumption increases, as they develop to later instar stages. During the intermolt intervals spiderlings require ample food to enable them to develop into the next stage (Foelix 1996). However, feeding slowed down before molting. This occurs naturally in all spiders. Foelix (1996) stated that most spiders that were preparing to molt withdraw into their retreat for several days and stop feeding. The success of rearing *C. inclusum* and *T. volutus* from egg to maturity using *P. citrella* alone as the source of food is an indication that these spiders do not require a varied food supply as compared to *H. velox*. Evidently, *H. velox* requires a varied food supply to complete its developmental cycle. Greenstone (1979) and Uetz et al. (1992) reported that certain spiders must feed on a variety of insect prey species to obtain the optimum nutrition for survival. This may also hold true for *H. velox*.

The results obtained from this study provide useful data to better understand the role of spiders in the overall management of *P. citrella* populations. Detailed observations on the predatory behavior of these three species of sac spiders showed that they exhibited a specialized feeding behavior in which they can search and extract a cryptic food source. This predatory behavior may merit their consideration as important predators of *P. citrella*, and they perhaps should be considered in the natural enemy complex of *P. citrella*. This potential can be realized only if these beneficial predators are fostered by orchard care practices.

ACKNOWLEDGMENTS

LITERATURE CITED

Amalin, D.M. 1999. Evaluation of predatory spiders as biological control agents of citrus leafminer, *Phyllocnistis citrella*, in lime orchards at Homestead, Florida. Ph.D. thesis. University of Florida, Gainesville, Florida.

Amalin, D.M., J.E. Peña & R. McSorley. 1995. Abundance of spiders in lime groves and their potential role in suppressing the citrus leafminer population. P. 72, *In* Proceedings, International Meeting: Managing the Citrus Leafminer (22–25 April 1996, Orlando, Florida (M.A. Hoy, ed.))., University of Florida, Gainesville, Florida.

Argov, Y. & Y. Rossler. 1996. Introduction, release and recovery of several exotic natural enemies for biological control of the citrus leafminer, *Phyllocnistis citrella*, in Israel. Phytoparasitica 24:33–38.

Bleckmann, H. & J.S. Rovner. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). I. Roles of vegetation and wind gathered waves in site selection. Behavioral Ecology and Sociobiology 14:297.

Borror, D.J., C.A. Triplehorn & D.M. Delong. 1992. Study of Insects (6th ed.). Saunders College Publishing. New York.

Bristowe, W.S. 1971. The World of Spiders. New Naturalist, London.

Browning, H. & J.E. Peña. 1995. Biological control of the citrus leafminer by its native parasitoids and predators. Citrus Industry 76:46–48.

Burgeous, W.J. & R.J. Constantin. 1995. Preliminary investigation into the control of citrus leafminer. Louisiana Agriculture 38:13–14.

Edwards, R.J. 1958. The spider subfamily Clubioninae of the United States, Canada, and Alaska (Araneae: Clubionidae). Bulletin of the Museum of Comparative Zoology 118:365–434.

Foelix, R.F. 1996. Biology of Spiders (2nd ed.). Oxford Univ. Press, Oxford.

Greenstone, M.H. 1979. Spider feeding behavior optimizes dietary essential amino acid composition. Nature 282:501–503.

Heppner, J.A. 1995. Citrus leafminer (Lepidoptera: Gracillariidae) on fruit in Florida. Florida Entomologist 78:183–186.

Heppner, J.B. 1993. Citrus leafminer, *Phyllocnistis citrella*, in Florida (Lepidoptera: Gracillariidae: Phyllocnistinae). Tropical Lepidoptera 4:49–64.

Jackson, R.R. 1977. Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). Animal Behaviour 25:953.

Knapp, J., L.G. Albrigo, H.W. Browning, R.C. Bullock, J. Heppner, D.G. Hall, M.A. Hoy, R. Nguyen, J.E. Peña & P. Stansly. 1995. Citrus leafminer, *Phyllocnistis citrella* Stainton: Current Status in Florida –1995. Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida.

Land, M.F. 1985. The morphology and optics of spider eyes. Pp. 53–78, *In* Neurobiology of

Arachnids. (F.G. Barth, ed.). Springer-Verlag, Berlin.

Platnick, N. 1974. The spider family Anyphaenidae in America North of Mexico. Bulletin of the Museum of Comparative Zoology 146:205–266.

Roth, V.D. 1993. Spider Genera of North America: With Keys to Families and Genera and a Guide to Literature. American Arachnological Society, Gainesville, Florida.

Rovner, J.S. 1978. Adhesive hairs in spiders: Behavioral functions and hydraulically mediated movement. Symposia of the Zoological Society, London 42:99.

SAS Institute. 1989. SAS/STAT User's guide, version 6, 3rd ed. Vol. 2. SAS Institute Inc. Cary, North Carolina.

Seyfart, E.A. 1980. Daily pattern of locomotory activity in a wandering spider. Physiological Entomology 5:199.

Uetz, G.W., J. Bischoff & J. Rover. 1992. Survivorship of wolf spiders (Lycosidae) reared on different diets. Journal of Arachnology 20:207–221.

Zhang, A., C. O'Leary & W. Quarles. 1994. Chinese IPM for citrus leafminer. Update. IPM Practitioner 16:10–13.

Zhao, J.C. 1989. Preservation and Application of Lacewings. Wuchang Univ. Press. Wuchang. Huber Province.

VARIATION IN THE CHEMICAL COMPOSITION
OF ORB WEBS BUILT BY THE SPIDER *NEPHILA CLAVIPES*
(ARANEAE, TETRAGNATHIDAE)

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ABSTRACT.   The adhesive droplets in the orb webs of araneoid spiders contain, among other constituents, an aqueous solution of organic low-molecular-weight compounds. The chemical composition of this solution has been investigated for pooled web collections from several species, but little is known about how the composition might vary among individuals or among environments. To begin addressing these questions, we analyzed serial collections of orb webs spun by individual juvenile *Nephila clavipes* from three different populations held first under field conditions and then under laboratory conditions.

Our results indicate that the composition of the organic low-molecular-weight solution is not fixed. We found significant differences in the droplet composition among individuals, among populations, and with the transfer of spiders to laboratory conditions. The possible origins and consequences of these differences are discussed.

Keywords: Orb web chemistry, interpopulational variation, intrapopulational variation, compatible solutes, adhesive spiral

Ecribellate orb-weaving spiders invest physiologically important compounds in the construction of their webs, including some that are nutritionally essential (i.e., not synthesized by the spider in sufficient quantity to meet its needs). This is particularly true for the adhesive spiral of the orb. Not only is the majority of the web's desiccated weight typically contributed by the adhesive spiral, but presumed essential amino acids make up a relatively large molar percentage of the proteins of the adhesive spiral (Tillinghast & Townley 1994). Also, at least one component of the aqueous solution on the adhesive spiral, choline, is nutritionally essential in insects (Dadd 1985) and evidence to date indicates that this is also true for araneoid orb-weavers, including *Nephila clavipes* (Linnaeus 1767) (Araneae, Tetragnathidae) (Tillinghast & Townley 1994; Higgins & Rankin 1999). Thus, the factors and mechanisms controlling the allocation of physiologically important compounds to

adhesive spiral construction are by no means inconsequential to the spider's fitness, as they have a direct impact on both orb web function and the spider's physiological state.

The adhesive spirals of ecribellate orb webs are composed of a pair of core fibers of flagelliform gland origin upon which an aqueous, adhesive coating of aggregate gland origin is deposited (Sekiguchi 1952; Peters 1955). Components of this adhesive coating include, but are not necessarily limited to, inorganic ions (Fischer & Brander 1960; Schildknecht et al. 1972), at least one large phosphorylated glycoprotein (Tillinghast 1981; Dreesbach et al. 1983; Vollrath & Tillinghast 1991; Tillinghast et al. 1993), lipids (Peters 1995, Schulz 1997), and organic low-molecular-weight compounds (LMW) (Fischer & Brander 1960). Collectively, the organic LMW are present in high concentration (Vollrath et al. 1990) and typically account for 30% or more of the desiccated weight of the orb

web (Fischer & Brander 1960; Tillinghast 1984; Tillinghast & Christenson 1984; Townley et al. 1991). Several of these are identical or closely related to compounds employed as osmolytes in various osmotically-stressed organisms of wide taxonomic distribution (see Discussion).

Within the last decade, nuclear magnetic resonance spectroscopy (NMR) has been applied to the study of the organic LMW of the adhesive spiral, both as a means for identifying compounds and for estimating their relative molar proportions in the sticky coating (Vollrath et al. 1990; Townley et al. 1991). These analyses used laboratory-built, pooled web samples from multiple individuals and were designed neither to examine compositional variation among individuals, nor to examine potential factors influencing organic LMW composition. As a first step along these lines of inquiry, we have used proton NMR to compare webs collected in the field and in the laboratory from individual *N. clavipes* from three disjunct populations. In this way, we examined variation among individuals within a population and among populations, and the sensitivity of organic LMW composition to changes in environment and diet, such as occur when spiders are brought into the laboratory.

Previously, organic LMW components of the adhesive coating in webs of *N. clavipes* have been shown to include 4-aminobutyramide (GABamide), glycine, and a compound yielding taurine upon acid hydrolysis (Tillinghast & Christenson 1984), now known to be *N*-acetyltaurine (Vollrath et al. 1990). Here we report that choline and glycine betaine, earlier identified in the webs of four araneid species (Vollrath et al. 1990), are also present in webs of *N. clavipes,* as are two compounds not previously reported in orb web adhesive spiral coatings, putrescine and alanine. In comparing field- and laboratory-built webs, we have focused our attention on quantitative analysis of these seven compounds. Our results indicate that organic LMW composition changes significantly when spiders are moved to the laboratory, that there is significant variation among individuals in the same environment, and that there are significant differences among populations in the wild.

METHODS

Study species.—*Nephila clavipes* is a large orb-weaving spider distributed from the southeastern United States to Misiones, Argentina. Males mature after 4–5 juvenile instars, females mature after 7–10 juvenile instars. Penultimate instar males can be distinguished from juvenile females by swollen pedipalps. Juveniles of 0.5 cm leg I tibia + patella length (fifth instar) that did not have swollen pedipalps were assumed to be juvenile females. Voucher specimens from all three study populations have been deposited at the Smithsonian Institution.

Handling spiders.—Fifteen 4–7th instar *N. clavipes* were collected in each of three sites (Los Tuxtlas, Mexico; Chamela, Mexico; and Brazos Bend, Texas, USA; Table 1) the evening before starting the experiment and placed into redwood boxes (26 cm × 24 cm × 8 cm) that had screen on the four narrow sides and sliding acrylic plastic sheeting ("Plexiglass"®) doors front and back. In all sites, the boxes were put along an edge between open and wooded habitats. At dawn, the Plexiglass doors were removed, allowing the spiders to capture prey in a normal fashion. However, if a spider had not built, or if it was premolt (as indicated by abdomen volume and web condition; Higgins 1990), the box was left closed. At dusk, each web with a vertical radius length greater than 10 cm was collected (see below), and the Plexiglass doors were replaced. In Mexico (Los Tuxtlas and Chamela), the boxes were moved at night and during heavy rainstorms (nearly every afternoon) to a sheltered area to protect the webs from rainfall damage. They were moved back out again after rainfall. Although we moved the boxes during the afternoon storms, we left them open to allow prey capture.

When at least five webs had been collected from each spider, all were moved in their boxes into the laboratory. In Mexico, the spiders were moved to the Institute of Ecology of the National Autonomous University (UNAM) in Mexico City, where they were held in an unheated, uncooled indoor room with windows admitting natural light. In Texas, the spiders were moved to the University of Texas at Austin, where they were kept in a climate controlled chamber (14:10 L:D, 25 °C). Each day in the laboratory, they were offered water

Table 1.—Characteristics of the study sites. TX: Austin, Texas; MX: Mexico City, Mexico. (Data from: Garcia 1973; S. H. Bullock personal communication; Texas Department of Parks personal communication).

Site	Coordinates	Annual rainfall (mm)	Laboratory diet	Laboratory conditions
Brazos Bend	29°25′N 95°35′W	1120	crickets	growth chamber (TX)
Los Tuxtlas	18°30′N 95°W	4400	crickets	normal room (MX)
Chamela	19°30′N 105°W	700	flies	room (MX), chamber (TX)

from a syringe and fed a monotypic diet (one cricket per day for animals from Texas and Los Tuxtlas, one housefly per day for animals from Chamela as crickets were not available). For the first wk under these conditions, spiders were allowed to recycle their webs. Subsequently, while maintaining the same feeding and watering regimen, webs were collected each day until at least five had been collected from each animal (but note the following exception).

Due to unforeseen circumstances, the laboratory treatment of Chamela spiders was interrupted before all animals had spun five orb webs. Therefore, these spiders were transported to Austin. Some of these spiders spun five or more orbs in both Texas and Mexico, allowing us to compare Mexico laboratory- and Austin laboratory-spun orb webs from the same individuals.

Handling orb webs.—The orb webs were collected each evening onto a clean glass rod (6.35 mm × 30.5 cm; one rod per spider per treatment—laboratory or field). The orbs were collected by cutting radii with a clean scalpel (wiped with 50% ethanol between samples), collapsing the orb, then winding it upon a section of the rod not already occupied by a previously collected web. Rods were stored suspended inside transparent PVC pipes, with a cork at each end having a hollow place for the rod to rest.

Orb web extraction.—After all webs for a given treatment had been collected, each web was scraped off of the rod with a clean razor blade and was placed in its own microfuge tube. The orb webs were washed twice in 50 μL distilled, deionized water (first wash 6 h, second wash 16 h; without agitation at room temperature). The web washes from a given treatment from a given spider were then combined and taken to dryness in a Savant Speed Vac concentrator. These specimens were

shipped to the University of New Hampshire for analysis by ^{1}H NMR.

^{1}H NMR analysis and LMW identification.—Each pooled web wash sample was dissolved in 0.5 mL 99.96% D_2O (Cambridge Isotope Laboratories) and analyzed by ^{1}H NMR using a Bruker AM-360 spectrometer with a 5 mm proton selective probe operating at a frequency of 360.135 MHz and a temperature of 300 K. An internal standard of 2-methyl-2-propanol, with a chemical shift of $\delta 1.2200$(ppm), was added to each sample just prior to NMR analysis. At a spectral width of 5000 Hz, 64K data points were acquired and an additional 64K data points with zero amplitude were appended to these (i.e., zero filled to 128K) prior to Fourier transformation to improve digital resolution in the frequency spectrum. Pulse width was 4.3 μsec (*ca.* 53°), acquisition time was 6.55 sec and pulse repetition time (τ) was 8.28 sec. The number of transients accumulated varied depending on sample size, ranging from about 300–8500, with about 1000 typical. Integrated peak areas in the frequency spectra were used to calculate the molar percentages of seven organic LMW in the web washes (*N*-acetyltaurine, 4-aminobutyramide (GABamide), glycine, choline, putrescine, glycine betaine, alanine).

Five of the LMW quantitatively studied have previously been reported in aggregate gland secretions of other araneoid species (Fischer & Brander 1960; Tillinghast & Christenson 1984; Vollrath et al. 1990). Identification of alanine resulted from a screening of various amino acids by ^{1}H NMR and was confirmed by analyzing web washes before and after the addition of alanine. Proline, a minor constituent detected in some web washes, was identified in the same way. Putrescine has been previously identified in web washes from the colonial araneid *Metepeira incrassata* via

partial purification and NMR analysis (Townley & Tillinghast pers. obs.).

Data analysis.—¹H NMR analysis provided the molar percentage of each of the seven LMW measured quantitatively (not necessarily totalling 100%, as these seven LMW were not the only identified organic LMW in web washes; see Qualitative variation section in Results). LMW composition was determined for no more than 11 individuals under both treatments from each population because of predation and natural mortality, together with failure to spin large enough webs (only webs with longest radius > 10 cm were collected). Laboratory conditions varied among the three populations studied (Table 1) and it is not possible to do a single statistical analysis testing for differences between the field and laboratory collected webs among all populations. Therefore, separate comparisons were made, three testing for an effect of environment (field *vs.* laboratory) within each population and one testing for differences among the field-collected webs of the three populations. The data were analyzed using multiple analysis of variance (MANOVA) with the GLM module of SYSTAT (Wilkinson 1992). Because percentages are not normally distributed, all data were arcsin (squareroot) transformed prior to analysis. Transformed molar percentages of the seven LMW were the dependent variables and either location (field *vs.* laboratory) or population was the independent variable. Similarly, MANOVA was used to compare the LMW composition of webs spun by Chamela spiders in the laboratory in Mexico City with those spun in the laboratory in Austin.

There are indications that juvenile males often build webs that are chemically distinct from webs of females. However, there were too few males from any one site (Los Tuxtlas, 2♂; Chamela, 2♂; Brazos Bend, 3♂) and sex was not included in the analysis as an independent variable.

RESULTS

The chemical composition of the aqueous solution of the adhesive spiral varied among individuals both qualitatively, with differences in which compounds were found, and quantitatively, with differences in the relative amounts of the compounds. Comparisons between field and laboratory web chemistry are based upon analysis of 58 web collections from 29 spiders that spun at least five webs under both field and laboratory conditions. In addition, comparisons between webs spun in Mexico City and Austin laboratories are based upon analysis of webs from eight spiders from Chamela. Below, we present first a description of the qualitative differences found among individuals between treatments and among populations, then a description of the quantitative differences found when seven major organic components of the aqueous solution are considered.

Qualitative variation.—Most of the individuals in all three populations spun webs containing all seven of the organic LMW that we examined quantitatively (*N*-acetyltaurine, GABamide, glycine, choline, putrescine, glycine betaine, alanine). *N*-acetyltaurine, choline and glycine betaine were invariably detected in web washes. Occasionally, one or more of the other four compounds was not detected by ¹H NMR (Table 2). Most notably, GABamide, typically a major constituent, was not detected in nine web collections built by six spiders. Putrescine, glycine and alanine each went undetected in at least one web collection. A disproportionately high percentage of such compound-deficient webs were obtained from juvenile males (Table 2).

While the seven measured LMW constitute a large percentage of the organic LMW (we estimate about 80–90% typically), they are not the only organic LMW in the viscid coating of *N. clavipes* adhesive spirals. Two compounds observed in some web washes, taurine and 4-aminobutyric acid (GABA) (Table 2), are presumed precursors of *N*-acetyltaurine and GABamide, respectively. Taurine was present in sizable quantity (9–14 mole %) only in laboratory-collected webs from two male Chamela spiders. These webs were also characterized by relatively low or undetectable levels of GABamide and glycine. Detectable amounts of GABA (2–15 mole %) were observed in 9 web collections, all but one from Brazos Bend, Texas.

A compound indistinguishable by ¹H NMR from acetate occurred in several Chamela web washes in the range of 3–17 mole % (Table 2). All of these web washes contained little or no detectable GABamide. Several other web washes of spiders from Chamela and Los Tuxtlas also appeared to contain small amounts of

Table 2.—Qualitative variation in the composition of *Nephila clavipes* web washes examined in this study. The identification numbers of the individual spiders exhibiting a given web composition feature are given in parentheses below non-zero values. [1] Field and laboratory web collections were obtained from 6 females and 3 males from Brazos Bend. Following collection of webs in the laboratory, the spiders were killed en masse by freezing before the sex of each numbered individual was determined. Thus, we do not know the sex of each individual. [2] F = field-collected; LM = laboratory-collected in Mexico City; LA = laboratory-collected in Austin. [3] An unidentified compound producing a singlet at 4.30 ppm in ^{1}H NMR spectra of some web washes. See Qualitative variation section of Results.

Population:	Chamela, Mexico						Los Tuxtlas, Mexico				Brazos Bend, Texas	
Sex:	male			female			male		female		male & female[1]	
Location[2]:	F	LM	LA	F	LM	LA	F	LM	F	LM	F	LA
# of web washes analyzed:	2	2	2	9	6	11	2	2	7	7	9	9
# lacking GABamide	1 (C14)	2 (C10, 14)	1 (C14)	1 (C12)	0	0	2 (T3, 6)	1 (T6)	0	0	0	1 (B15)
# lacking putrescine	0	0	0	0	0	0	2 (T3, 6)	0	1 (T13)	0	0	0
# lacking glycine	0	0	1 (C14)	0	0	0	0	0	0	0	0	0
# lacking alanine	0	0	1 (C14)	0	0	0	0	0	0	0	1 (B15)	0
# with taurine (≥9 mole %)	0	1 (C14)	2 (C10, 14)	0	0	0	0	0	0	0	0	0
# with GABA (≥2 mole %)	0	0	0	1 (C16)	0	0	0	0	0	0	4 (B1, 6, 8, 10)	4 (B, 1, 6, 10, 15)
# with acetate (≥3 mole %)	2 (C10, 14)	1 (C10)	0	1 (C12)	0	0	0	0	0	0	0	0
# with 4.30 ppm compound[3]	0	0	0	0	0	0	0	0	0	0	8 (B1, 3, 4, 5, 6, 8, 10, 11)	1 (B4)

Table 3.—Pearson correlation matrices for each population, including both field and laboratory collected webs. The molar percentage of each compound was arcsin (squareroot) transformed prior to analysis. Abbreviations: gly = glycine; N-tau = N-acetyltaurine; GABam = GABamide; put: putrescine; cho = choline; bet = glycine betaine. Bonferroni-corrected P-values: * $P \leq 0.05$, ** $P \leq 0.001$.

Los Tuxtlas

	gly	N-tau	GABam	put	cho	bet
N-acetyltaurine	−0.941**					
GABamide	0.735*	−0.833**				
putrescine	0.508	−0.678*	0.341			
choline	−0.221	0.186	−0.484	0.259		
glycine betaine	−0.528	0.656	−0.712*	−0.490	0.230	
alanine	0.538	−0.512	0.399	0.111	−0.149	0.067

Chamela

	gly	N-tau	GABam	put	cho	bet
N-acetyltaurine	−0.847**					
GABamide	0.451	−0.529				
putrescine	−0.214	0.001	−0.401			
choline	−0.375	0.320	−0.846**	0.496		
glycine betaine	−0.304	0.449	−0.889**	0.338	0.797**	
alanine	0.795**	−0.804**	0.530	−0.024	−0.425	−0.360

Brazos Bend

	gly	N-tau	GABam	GABA	put	cho	bet
N-acetyltaurine	−0.736*						
GABamide	0.133	−0.562					
GABA	0.227	0.070	−0.626				
putrescine	−0.703*	0.724*	−0.597	0.012			
choline	−0.656	0.855**	−0.683*	0.047	0.843**		
glycine betaine	−0.191	0.398	−0.428	0.129	0.058	0.416	
alanine	0.362	−0.444	0.178	−0.249	−0.135	−0.252	−0.495

acetate (< 1 mole %). Proline was detected in web washes from individuals of all three populations. Those web washes containing sufficient proline to allow certain identification were from webs built by females in the laboratory. Proline accounted for no more than 3 mole % of the organic LMW.

Some additional organic LMW have not been identified. Most notable is a compound producing a sometimes prominent singlet (at most, peak area comparable to that of N-acetyltaurine's singlet) at 4.30 ppm in ¹H NMR spectra, observed in all but one of the field-built web collections from the Brazos Bend population. Again with a single exception, this compound was absent from the laboratory-built web collections from this population and in the one exception, it was present in lower relative quantity than was observed in the field-collected webs. It was not observed at all in the two Mexican populations studied (Table 2).

Quantitative variation.—There were some strong correlations among the seven LMW analyzed in this study (N-acetyltaurine, GABamide, glycine, choline, putrescine, glycine betaine and alanine; Table 3). Among all three populations, the amount of N-acetyltaurine was negatively correlated with the amount of glycine. There was a tendency for a negative correlation of GABamide with glycine betaine (not significantly for Brazos Bend), choline (not significantly for Los Tuxtlas) and N-acetyltaurine (significant only for Los Tuxtlas). Between pairs of chemically similar compounds, the amounts of choline and glycine betaine and the amounts of glycine and alanine tended to be positively associated, although these relationships were significant only for webs spun by Chamela spiders. No significant correlation was found between glycine and glycine betaine. There was a non-significant trend toward a negative correlation of the amount of GABA (common only in webs of spiders from Brazos Bend) with the amount of its derivative, GABamide.
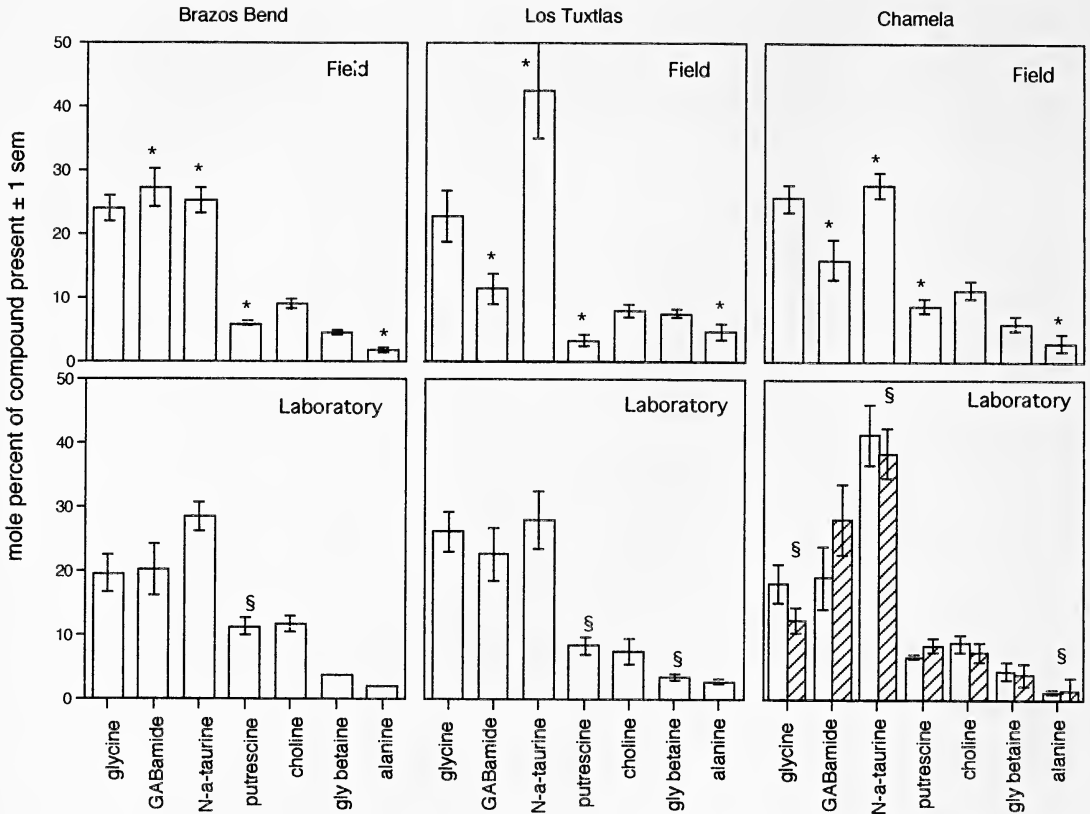
Figure 1.—The average molar percentage of each of the seven studied low-molecular weight organic compounds (± SEM) for each population under field and laboratory conditions. Data from Chamela include observations made in the laboratory in Mexico City (open bars) and in the laboratory in Austin (hatched bars). N-a-taurine: N-acetyltaurine; gly betaine: glycine betaine. ⋆ = Significant difference (P ≤ 0.05) among populations; § = significant difference (P ≤ 0.05) between field and laboratory conditions within a population (Bonferroni -corrected P values).

Testing for significant patterns of variation in these components among populations and between field and laboratory conditions involved multivariate analysis of variance of arcsin (square root) transformed relative quantities of the seven primary compounds (mole %; Fig. 1). Separate tests were done to examine patterns of variation among webs from different sites and, within a population, between field- and laboratory-spun webs.

There were significant quantitative differences in LMW composition among webs collected from different field sites (Fig. 1, Table 4). Examination of the univariate F tests for the individual components shows that the molar percentages of N-acetyltaurine and alanine were significantly higher and putrescine was lower in webs spun at Los Tuxtlas compared to the other two sites (N-acetyltaurine: $F_{(2, 26)}$

= 4.274, P = 0.025; alanine: $F_{(2, 26)}$ = 3.898, P = 0.033; putrescine: $F_{(2, 26)}$ = 9.129, P = 0.001). The webs spun at Brazos Bend had higher relative amounts of GABamide than those from the other two sites ($F_{(2, 26)}$ = 4.878, P = 0.016). Variation in the molar percentages of choline and glycine betaine was nearly significant (P ≤ 0.06).

The relative quantities of these components of the LMW solution changed when spiders were moved from the field to the laboratory (Fig. 1). Analyzing the data for each population separately (Table 4), the spiders from Chamela and Los Tuxtlas significantly altered the composition of the LMW, and the spiders from Chamela further altered the web chemistry when they were moved from the laboratory in Mexico City to Austin. The spiders from Brazos Bend showed non-significant

Table 4.—Multiple analysis of variance: Differences among field-spun webs from spiders in three populations, and differences between field- and laboratory-spun webs from three populations. The two entries for Chamela field to laboratory comparisons reflect comparisons between field and the laboratory in Mexico (F/LM) and between field and the laboratory in Austin (F/LA).

	Wilk's lambda	F-statistic	Degrees of freedom	P value
Among field-spun webs				
	0.190	3.700	14, 40	0.001
Between field- and laboratory-spun webs				
Brazos Bend	0.335	2.835	7, 10	0.066
Los Tuxtlas	0.130	9.578	7, 10	0.001
Chamela F/LM	0.051	10.73	7, 14	0.018
Chamela F/LA	0.085	21.54	7, 14	<0.001
Between laboratory settings				
Chamela	0.193	4.767	7, 8	0.022

shifts in the relative amounts of the seven compounds.

The changes in LMW composition accompanying the move from field to laboratory differed among the three populations. Spiders from Los Tuxtlas increased putrescine and decreased glycine betaine (putrescine: $F_{(1, 16)}$ = 10.36, P = 0.005; glycine betaine: $F_{(1, 16)}$ = 22.58, $P < 0.001$). The spiders from Chamela decreased free alanine when moved from the field into the laboratory in Mexico City and this change persisted when the spiders were moved to Austin (field vs. lab in Mexico: $F_{(1, 10)}$ = 8.92, P = 0.014; field vs. lab in Austin: $F_{(1, 20)}$ = 10.645, P = 0.004). Comparison of the field webs with the webs spun in Austin also showed a decline in the percentage of glycine and an increase in N-acetyltaurine (glycine: $F_{(1,20)}$ = 19.22, $P < 0.001$; N-acetyltaurine: $F_{(1, 20)}$ = 10.417, P = 0.004). The significant change in composition between the webs spun by the Chamela spiders in the laboratory in Mexico City and in the laboratory in Austin reflects overall trends; no single component changed significantly. In the case of the Brazos Bend population, although the multivariate statistic was nonsignificant, there was a significant increase in the molar percentage of putrescine when the spiders were moved from the field into the laboratory ($F_{(1, 16)}$ = 14.705, P = 0.001).

In addition to the statistically significant changes, three trends are of interest because a majority of individuals from Los Tuxtlas or Chamela exhibited them. Relocation of Los Tuxtlas and Chamela females to the laboratory tended to result in decreased percentages of choline (7 of 7 from Los Tuxtlas, 12 of 13 from Chamela) and increased GABamide (7 of 7 field/laboratory comparisons from Los Tuxtlas, 12 of 13 from Chamela). Males from these populations (albeit a small sample size) did not exhibit these trends: among males, choline concentration tended to increase and GABamide tended to decrease with relocation to the laboratory. N-acetyltaurine percentages changed in opposite directions in the webs of individuals from these populations: Los Tuxtlas animals, male and female, tended to decrease the percentage of this compound (8 of 9) whereas, as mentioned above, the percentage increased significantly on webs built by male and female Chamela spiders in the laboratory relative to webs built in the field (17 of 17).

¹H NMR spectral data.—Data for GABamide, N-acetyltaurine, glycine, choline, glycine betaine, and taurine have been published (Townley et al. 1991). The additional LMW identified in this study yielded the following ¹H NMR spectral data in D_2O (chemical shifts in ppm, with the methyl hydrogens of the internal standard, 2-methyl-2-propanol, assigned a chemical shift of δ1.2200): acetate, singlet at δ1.88; alanine, quartet at δ3.75 (J = 7.3 Hz), doublet at δ1.45 (J = 7.3 Hz); GABA, triplets at δ2.99 (J = 7.5 Hz), δ2.27 (J = 7.3 Hz), quintet at δ1.87 (J = 7.4 Hz);

proline, multiplets at δ4.10, δ3.35 (δ3.40, δ3.30), δ2.31, δ2.01; putrescine, multiplets at δ3.02, δ1.73.

DISCUSSION

The current study extends previous reports on the chemical composition of the organic LMW solution found on ecribellate adhesive spirals by documenting variation in web chemistry within and among populations. Furthermore, we observed significant quantitative shifts in LMW composition correlated with changes in environment: the spiders from the two Mexican populations significantly altered relative amounts of some LMW on their webs when moved from the field into the laboratory. Examination of webs spun by individuals also revealed patterns of individual qualitative variation in the composition of the LMW solution. Some spiders, particularly juvenile males, spun webs in which compounds characteristic of *N. clavipes* webs were undetected and/or novel compounds were found. Following a discussion of the extrinsic and intrinsic factors that may singly or in combination result in spiders spinning webs with different LMW composition, we discuss the possible influence of LMW composition on web function.

There are four possible factors that may influence the chemistry of the LMW portion of the web: physical environment, diet, web recycling, and ontogenetic changes in web chemistry. First, if physical properties of the adhesive spiral (e.g., hygroscopicity, droplet viscosity, extensibility) are influenced by LMW composition, it seems unlikely that a single LMW composition would prove ideal in all environments inhabited by individuals of one species. Thus, there is the possibility that among-population differences in LMW composition and the shift in composition when individuals are moved from one environment to another may reflect individual spiders' adjustments to the conditions of the physical environment. Among-population differences may also reflect genetic differences among populations, as selection favors different chemical and physical properties in different physical environments. Second is the possibility that qualitative differences in diet affected LMW composition as spiders were shifted from the field to the laboratory. These spiders eat a variety of prey in the field (Hig-

gins & Buskirk 1992), but were kept on a monotypic diet in the laboratory. As prey types vary among these three populations in the field (Higgins pers. obs.), qualitative dietary differences may contribute to among-population differences as well. Qualitative changes in diet have been found to alter amino acid composition of spider major ampullate silk (Craig et al. in press). Third, we now have evidence that web recycling influences LMW composition (Townley & Tillinghast pers. obs.) and recycling was an uncontrolled variable between the field and laboratory portions of the study. Spiders were collected from intact orb webs and the first web built in the field portion of the study, also the first web collected, presumably included little recycled material. In contrast, the spiders recycled the orb prior to collection of the first web in the laboratory. Last, there is the possibility of ontogenetic changes in LMW composition, independent of diet and environmental conditions. Ontogenetic changes in structural features of orb webs (e.g., number of radii, mesh size, shape) have been documented (Witt et al. 1972; Ramousse 1973; Eberhard 1985 and references therein; Eberhard 1986; Edmunds 1993) and it is possible that changes during development may extend to facets of web composition as well. Indeed, Osaki (1989) has reported changes in the color of major ampullate silk, presumably due to changes in chemical composition, with the approach of maturity in female *Nephila clavata*.

Differences in LMW composition could affect various physical properties of the adhesive spiral and, thereby, affect the web's prey-catching ability. Therefore, the possible functional consequences of qualitative and quantitative differences in adhesive spiral composition merit further examination. For example, some of the LMW are hygroscopic (Vollrath et al. 1990; Townley et al. 1991) and the overall hygroscopicity of the LMW mixture presumably varies with LMW composition. Differences in hygroscopicity may have an impact on web function because adsorption and retention of water by the adhesive spiral is essential to its adhesiveness, elasticity, and extensibility. Water's involvement in adhesive spiral functioning may be a combination of direct effects, due to interactions between water and adhesive spiral components, and indirect effects, due to interactions between

LMW and adhesive spiral macromolecules that require an aqueous medium (Richter 1956; Schildknecht et al. 1972; Vollrath & Edmonds 1989; Bonthrone et al. 1992; Edmonds & Vollrath 1992; Gosline et al. 1994, 1995; Hayashi & Lewis 1998).

Beyond the possible consequences for adhesive spiral hygroscopicity, LMW compositional differences may also influence the effectiveness of the adhesive spiral by affecting its macromolecular structure more directly. Here we briefly discuss three hypothetical ways in which the organic LMW may accomplish this: as compatible solutes, through direct interaction with macromolecules, and as counteracting solute systems.

A wide variety of procaryotic and eucaryotic cells subject to osmotic stress employ certain organic osmolytes to adjust intracellular osmolarity. These osmolytes are sometimes referred to as compatible solutes (Brown & Simpson 1972) because, unlike inorganic ions in most organisms, they can occur at high concentrations without perturbing, and even while stabilizing, protein structure (Yancey et al. 1982; Le Rudulier et al. 1984; Somero 1986, 1992; Csonka & Hanson 1991; Kinne 1993; Galinski 1993, 1995). Protein stabilization by compatible solutes has been attributed to the tendency of these solutes to be excluded from the immediate vicinity of protein surfaces (so increasing the non-uniform distribution of solute) and to exhibit low specific binding to proteins (Arakawa & Timasheff 1985; Timasheff 1992). Thus, these solutes promote processes of protein folding and subunit aggregation that minimize protein surface area and typically favor protein stability. Although the web is external, certain of the adhesive spiral's organic LMW (glycine, glycine betaine, alanine, proline, taurine) are identical to known compatible solutes (Townley et al. 1991). Thus, these compounds may, by the same mechanism, help stabilize the native conformation of adhesive spiral proteins.

One important distinction between compatible solutes and some of the LMW compounds on the adhesive spiral concerns molecular charge. Compatible solutes are usually uncharged or net neutral molecules, whereas several of the adhesive spiral LMW components (N-acetyltaurine, GABamide, choline, putrescine) carry a net charge and might be expected to show a greater tendency to interact with proteins. Such direct interactions between organic LMW and other components of the spiral strand, e.g., the adhesive glycoprotein(s) or core fiber proteins, may be vital for the proper functioning of these adhesive spiral strand macromolecules (Townley et al. 1991; Gosline et al. 1995).

The combination of solutes in the aqueous solution on the web's adhesive spiral may also function as a counteracting solute system, wherein the perturbing influence to native macromolecular structure by one or more destabilizing solutes is offset by the presence of other, stabilizing, i.e., compatible, solutes (Somero 1986; Timasheff 1992). The best studied example of such a system is the urea (destabilizer)/methylamine (stabilizer) system of marine cartilaginous fish, the coelacanth, and mammalian kidneys (Yancey et al. 1982; Somero 1986, 1992; Garcia-Perez & Burg 1991; Yancey 1992). On the web, the perturbing influence of inorganic ions and/or one or more of the organic LMW (especially net charged organic LMW) could be countered by other, stabilizing LMW. Optimal performance of adhesive spiral macromolecules in such a solute system may depend on the various LMW occurring at fairly specific concentration ratios to one another (Yancey et al. 1982; Somero 1986, 1992; Yancey 1992).

In all three of these chemical models, differences in LMW composition, such as those documented herein, may directly translate into differences in macromolecular structure, with consequences for the adhesive spiral's trapping ability. However, we must emphasize that at this time the ability of the web's organic LMW to affect macromolecular structure by any of the aforementioned mechanisms is speculative. Whether the observed differences in web chemistry reflect adaptive responses to the environment or simply non-adaptive plasticity (Via 1993), these changes in LMW composition could be important both for web function and for physiological function. Precursors or derivatives of the organic LMW, if not the LMW themselves, play important physiological roles (e.g., as neurotransmitters and in cell membrane phospholipids). However, orb-weaving spiders must invest LMW and other essential and non-essential compounds in the synthesis of the orb web because they are completely dependent upon the web for capturing prey. Although

web recycling allows the spider to recoup a portion of this investment (Breed et al. 1964; Peakall 1971; Townley & Tillinghast 1988), some loss of material is inevitable. Thus, with each web-building event, allocation "decisions" must be made; and there is experimental evidence for trade-offs in allocation of limited resources between foraging (the orb) and physiological demands (Higgins & Rankin 1999). Because orb-weaving spiders depend entirely on the web for capturing prey and because the synthesis of the orb web requires an investment of physiologically important compounds, this group of spiders could become a model system for investigating resource allocation (Benforado and Kistler 1973; Higgins 1990, 1992, 1995; Higgins & Buskirk 1992; Sherman 1994, Blackledge 1998; Herberstein et al. 2000).

The full realization of this potential will be facilitated by further investigation of orb web synthesis, recycling, and composition, particularly of the adhesive spiral, which, even neglecting water content, often makes a considerably greater contribution to web weight than the non-adhesive web elements.

ACKNOWLEDGMENTS

LITERATURE CITED

Arakawa, T. & S.N. Timasheff. 1985. The stabilization of proteins by osmolytes. Biophysical Journal 47:411–414.

Benforado, J. & K.H. Kistler. 1973. Growth of the orb weaver, *Araneus diadematus,* and correlation with web measurements. Psyche 80:90–100.

Blackledge, T.A. 1998. Stabilimentum variation and foraging success in *Argiope aurantia* and *Ar-*

giope trifasciata (Araneae: Araneidae). Journal of Zoology, London 246:21–27.

Bonthrone, K.M., F. Vollrath, B.K. Hunter & J.K.M. Sanders. 1992. The elasticity of spiders' webs is due to water-induced mobility at a molecular level. Proceedings of the Royal Society of London, B, Biological Sciences 248:141–144.

Breed, A.L., V.D. Levine, D.B. Peakall & P.N. Witt. 1964. The fate of the intact orb web of the spider *Araneus diadematus* Cl. Behaviour 23:43–60.

Brown, A.D. & J.R. Simpson. 1972. Water relations of sugar-tolerant yeasts: The role of intracellular polyols. Journal of General Microbiology 72:589–591.

Craig, C.L., C. Riekel, M.E. Herberstein, R.S. Weber, D. Kaplan & N.E. Pierce. In press. Evidence for diet effects on the composition of silk proteins produced by spiders. Molecular Biology and Evolution.

Csonka, L.N. & A.D. Hanson. 1991. Prokaryotic osmoregulation: Genetics and physiology. Annual Review of Microbiology 45:569–606.

Dadd, R.H. 1985. Nutrition: Organisms. Pp. 313–390. *In* Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 4, Regulation: Digestion, Nutrition, Excretion. (G.A. Kerkut & L.I. Gilbert, eds.). Pergamon Press, Oxford, UK.

Dreesbach, K., G. Uhlenbruck & E.K. Tillinghast. 1983. Carbohydrates of the trypsin soluble fraction of the orb web of *Argiope trifasciata.* Insect Biochemistry 13:627–631.

Eberhard, W.G. 1985. The "sawtoothed" orb web of *Eustala* sp. (Araneae, Araneidae) with a discussion of ontogenetic changes in spiders' web-building behavior. Psyche 92:105–117.

Eberhard, W.G. 1986. Ontogenetic changes in the web of *Epeirotypus* sp. (Araneae, Theridiosomatidae). Journal of Arachnology 14:125–128.

Edmonds, D.T. & F. Vollrath. 1992. The contribution of atmospheric water vapour to the formation and efficiency of a spider's capture web. Proceedings of the Royal Society of London, B, Biological Sciences 248:145–148.

Edmunds, J. 1993. The development of the asymmetrical web of *Nephilengys cruentata* (Fabricius). Memoirs of the Queensland Museum 33:503–506.

Fischer, F.G. & J. Brander. 1960. Eine Analyse der Gespinste der Kreuzspinne. Hoppe-Seyler's Zeitsschrift fuer Physiologische Chemie 320:92–102.

Galinski, E.A. 1993. Compatible solutes of halophilic eubacteria: Molecular principles, water-solute interaction, stress protection. Experientia 49:487–496.

Galinski, E.A. 1995. Osmoadaptation in bacteria. Advances in Microbial Physiology 37:273–328.

Garcia, E. 1973. Modificaciones al Systema de Clasificación Climatica de Köppen. Universidad

Nacional Autonoma de Mexico Press, Mexico City.

Garcia-Perez, A. & M.B. Burg. 1991. Renal medullary organic osmolytes. Physiological Reviews 71:1081–1115.

Gosline, J., C. Nichols, P. Guerette, A. Cheng & S. Katz. 1995. The macromolecular design of spiders' silks. Pp. 237-261, In Biomimetics: Design and Processing of Materials. (M. Sarikaya & I.A. Aksay, eds.). American Institute of Physics Press, Woodbury, New York.

Gosline, J.M., C.C. Pollak, P.A. Guerette, A. Cheng, M.E. DeMont & M.W. Denny. 1994. Elastomeric network models for the frame and viscid silks from the orb web of the spider Araneus diadematus. Pp. 328-341. In Silk Polymers. Materials Science and Biotechnology. (D. Kaplan, W.W. Adams, B. Farmer, C. Viney, eds.). American Chemical Society, Washington, D.C.

Hayashi, C.Y. & R.V. Lewis. 1998. Evidence from flagelliform silk cDNA for the structural basis of elasticity and modular nature of spider silks. Journal of Molecular Biology 275:773–784.

Herberstein, M.E., C.L. Craig & M.A. Elgar. 2000. Foraging strategies and feeding regimes: Web decoration investment in Argiope keyserlingi Karsh (Araneae: Araneidae). Evolutionary Ecology Research 2:69–80.

Higgins, L.E. 1990. Variation in foraging investment during the intermolt interval and before egg-laying in the spider Nephila clavipes (Araneae: Araneidae). Journal of Insect Behavior 3:773–783.

Higgins, L.E. 1992. Developmental changes in barrier web structure under different levels of predation risk in Nephila clavipes (Araneae: Tetragnathidae). Journal of Insect Behavior 5:635–655.

Higgins, L.E. 1995. Direct evidence for trade-offs between foraging and growth in a juvenile spider. Journal of Arachnology 23:37–43.

Higgins, L.E. & R.E. Buskirk. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. Animal Behaviour 44:485–499.

Higgins, L.E. & M.A. Rankin. 1999. Nutritional requirements for web synthesis in the tetragnathid spider Nephila clavipes. Physiological Entomology 24:263–270.

Kinne, R.K.H. 1993. The role of organic osmolytes in osmoregulation: From bacteria to mammals. Journal of Experimental Zoology 265:346–355.

Le Rudulier, D., A.R. Strom, A.M. Dandekar, L.T. Smith & R.C. Valentine. 1984. Molecular biology of osmoregulation. Science 224:1064–1068.

Osaki, S. 1989. Seasonal change in color of spiders' silk. Acta Arachnologia 38:21–28.

Peakall, D.B. 1971. Conservation of web proteins

in the spider, Araneus diadematus. Journal of Experimental Zoology 176:257–264.

Peters, H.M. 1955. Über den Spinnapparat von Nephila madagascariensis (Radnetzspinnen, Fam. Argiopidae). Zeitschrift fuer Naturforschung 10b:395–404.

Peters, H.M. 1995. Ultrastructure of orb spiders' gluey capture threads. Naturwissenschaften 82:380–382.

Ramousse, R. 1973. Body, web-building and feeding characteristics of males of the spider Araneus diadematus (Araneae: Araneidae). Psyche 80:22–47.

Richter, G. 1956. Untersuchungen über Struktur und Funktion der Klebefäden in den Fanggeweben ecribellater Radnetzspinnen. Naturwissenschaften 43:23.

Schildknecht, H., P. Kunzelmann, D. Krauß & C. Kuhn. 1972. Über die Chemie der Spinnwebe, I: Arthropodenabwehrstoffe, LVII. Naturwissenschaften 59:98–99.

Schulz, S. 1997. The chemistry of spider toxins and spider silk. Angewandte Chemie International Edition in English 36:314–326.

Sekiguchi, K. 1952. On a new spinning gland found in geometric spiders and its functions. Annotationes Zoologicae Japonenses 25:394–399.

Sherman, P.M. 1994. The orb-web: An energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. Animal Behaviour 48:19–34.

Somero, G.N. 1986. Protons, osmolytes, and fitness of internal milieu for protein function. American Journal of Physiology 251:R197–R213.

Somero, G.N. 1992. Adapting to water stress: Convergence on common solutions. Pp. 3–18. In Water and Life: Comparative Analysis of Water Relationships at the Organismic, Cellular, and Molecular Levels. (G.N. Somero, C.B. Osmond & C.L. Bolis, eds.). Springer-Verlag, Berlin.

Tillinghast, E.K. 1981. Selective removal of glycoproteins from the adhesive spiral of the spiders orb web. Naturwissenschaften 68:526–527.

Tillinghast, E.K. 1984. The chemical fractionation of the orb web of Argiope spiders. Insect Biochemistry 14:115–120.

Tillinghast, E.K. & T. Christenson. 1984. Observations on the chemical composition of the web of Nephila clavipes (Araneae, Araneidae). Journal of Arachnology 12:69–74.

Tillinghast, E.K., M.A. Townley, T.N. Wight, G. Uhlenbruck & E. Janssen. 1993. The adhesive glycoprotein of the orb web of Argiope aurantia (Araneae, Araneidae). Pp. 9–23. In Biomolecular Materials. (C. Viney, S.T. Case & J.H. Waite, eds.). Materials Research Society Symposium Proceedings, Vol. 292. Materials Research Society, Pittsburgh, Pennsylvania.

Tillinghast, E.K. & M.A. Townley. 1994. Silk glands of araneid spiders: Selected morphological and physiological aspects. Pp. 29–44. *In* Silk Polymers: Materials Science and Biotechnology. (D. Kaplan, W.W. Adams, B. Farmer & C. Viney, eds.). American Chemistry Society Symposium, Series 544. American Chemical Society, Washington, D. C.

Timasheff, S.N. 1992. A physicochemical basis for the selection of osmolytes by nature. Pp. 70–84. *In* Water and Life: Comparative Analysis of Water Relationships at the Organismic, Cellular, and Molecular Levels. (G.N. Somero, C.B. Osmond & C.L. Bolis, eds.). Springer-Verlag, Berlin.

Townley, M.A. & E.K. Tillinghast. 1988. Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component, GABamide. Journal of Arachnology 16:303–319.

Townley, M.A., D.T. Bernstein, K.S. Gallagher & E.K. Tillinghast. 1991. Comparative study of orb web hygroscopicity and adhesive spiral composition in three araneid spiders. Journal of Experimental Zoology 259:154–165.

Via, S. 1993. Adaptive phenotypic plasticity: Target or by-product of selection in a variable environment? American Naturalist 142:352–365.

Vollrath, F. & D.T. Edmonds. 1989. Modulation of the mechanical properties of spider silk by coating with water. Nature 340:305–307.

Vollrath, F., W.J. Fairbrother, R.J.P. Williams, E.K. Tillinghast, D.T. Bernstein, K.S. Gallagher & M.A. Townley. 1990. Compounds in the droplets of the orb spider's viscid spiral. Nature 345: 526–528.

Vollrath, F. & E.K. Tillinghast. 1991. Glycoprotein glue beneath a spider web's aqueous coat. Naturwissenschaften 78:557–559.

Wilkinson, L. 1992. SYSTAT: Statistics, Version 5.2 Edition. Systat, Inc., Evanston, Illinois.

Witt, P.N., J.O. Rawlings & C.F. Reed. 1972. Ontogeny of web-building behavior in two orb-weaving spiders. American Zoologist 12:445–454.

Yancey, P.H. 1992. Compatible and counteracting aspects of organic osmolytes in mammalian kidney cells in vivo and in vitro. Pp. 19–32. *In* Water and Life: Comparative Analysis of Water Relationships at the Organismic, Cellular, and Molecular Levels. (G.N. Somero, C.B. Osmond & C.L. Bolis, eds.). Springer-Verlag, Berlin.

Yancey, P.H., M.E. Clark, S.C. Hand, R.D. Bowlus & G.N. Somero. 1982. Living with water stress: Evolution of osmolyte systems. Science 217: 1214–1222.

PATTERNS OF ABUNDANCE OF FOUR SPECIES OF WANDERING SPIDERS (CTENIDAE, *CTENUS*) IN A FOREST IN CENTRAL AMAZONIA

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ABSTRACT. We studied spatial and temporal patterns of abundance of *Ctenus amphora*, *C. crulsi*, *C. manauara* and *C. villasboasi*, four syntopic species of medium-to-large sized wandering spiders that forage on the ground in a neotropical rainforest. We found temporal variation, apparently seasonal, in abundance for two of the four species. The four species are sympatric in the study area, but with very distinct spatial patterns of abundance. *Ctenus amphora* was more abundant in areas with sandy soil but are also common on clay soils, *C. manauara* and *C. crulsi* are the dominant species in areas with clay soil and are infrequent in sandy soils, and *C. villasboasi* had a more homogenous abundance in the study area. Previous studies suggested that a predator, army ants, could have an important impact on the abundance of these spiders. We estimated the frequency of attacks by army ants using pitfall traps in sandy and clay soil areas. The estimated probability of attack by army ants was higher in areas with clay soil (92% per 3 months), where all species are frequently found, than in sandy soil areas (21%), where *C. crulsi* and *C. manauara* were almost absent. However, it is still not clear if predation by army ants is a key factor that facilitates coexistence in clay soils, and this factor can not explain the difference on the dominant species between areas with different soil types. We also discuss the description of spatial patterns of abundance as a simple, but powerful, tool seldom used for preliminary studies on the coexistence of spiders.

RESUMO. Nós estudamos padrões espaciais e temporais de abundância de *Ctenus amphora*, *C. crulsi*, *C. manauara* e *C. villasboasi*, quatro espécies sintópicas de aranhas errantes que forageiam no chão em uma floresta neotropical úmida. Nós encontramos uma variação temporal, aparentemente sazonal, na abundafancia de duas das quatro espécies. As quatro espécies são simpátricas na área de estudo, mas com padrões espaciais de abundância muito distintos. *Ctenus amphora* foi mais abundante em áreas de solos arenosos, mas também foi comum em solos argilosos *C. manauara* e *C. crulsi* foram as espécies dominantes em solos argilosos, e foram infreqüentes em solos arenosos, e *C. villasboasi* teve uma abundância mais homogênea na área de estudo. Estudos anteriores sugeriram que um predador, formigas de correição, poderia ter um forte impacto sobre a abundância destas aranhas. Nós estimamos a freqüência de ataques por formigas de correição usando armadilhas de fosso (pitfall traps) em áreas de solo arenoso e argiloso. A probabilidade estimada de ataques por formigas de correição foi maior em áreas de solo argiloso (92% em 3 meses), onde todas as espécies são freqüentemente encontradas, que em solo arenoso (21%), onde *C. crulsi* e *C. manauara* foram raras. Entretanto, ainda não está claro se a predação é um fator chave para facilitar a coexistência em solos argilosos, e este fator não pode explicar a diferença de espécies dominantes entre as áreas com tipos de solo diferentes. Nós também discutimos a descrição de padrões espaciais de abundância como um ferramenta simples, mas poderosa e pouco usada para o estudo da coexistência de aranhas.

Keywords: Army ants, predation, coexistence, method

Studies on the ecology of wandering spiders have been performed mainly in temperate regions and mostly with spiders of the family Lycosidae (e.g., Edgar 1971a, b; Ford 1977, 1978; Greenstone 1978, 1979, 1980; Hallander 1970 a, b; Suwa 1986; Van Dyke & Lowrie 1975; Wise 1993). Although the family Ctenidae is rich in species and abundant in the tropics, there are few studies on their ecology. One exception is the genus *Cupiennius*, which

was intensively studied by Barth and collaborators (e.g., Schuster et al. 1994 and citations in it); however, in this genus only the males are considered wandering spiders (Schmitt et al. 1990).

Höfer, Brescovit & Gasnier (1994) studied the wandering spiders of the genus *Ctenus* (Walckenaer 1805) in "Reserva Florestal Adolfo Ducke" (RFAD) in central Amazonia. They found seven species, four of which (*Ctenus amphora* Mello-Leitão 1930; *C. crulsi* Mello-Leitão 1930; *C. manauara* Höfer, Brescovit & Gasnier 1994; and *C. villasboasi* Mello-Leitão 1949) are very similar in behavior and use of microhabitat. They forage in and on the leaf litter and are the dominant medium-to-large sized wandering spiders on the ground in most parts of this forest.

Vieira & Höfer (1994, 1998) studied swarm-raiding army ants (*Eciton burchelli* and *Labidus praedator*) in central Amazonia (100 km north of RFAD) and concluded that the spiders of the genus *Ctenus* are among the major prey items of these ants. The effect of army ants on ground-living spiders, including *Ctenus*, was also discussed by Gasnier, Höfer & Brescovit (1995). These ants forage in massive groups of many thousands of individuals, and these authors suggest that they probably have a strong impact on the abundance and on the structure of this guild of wandering spiders. However, although *Ctenus* is an important prey for army ants, the impact of the ants on the spiders is unknown because there is no estimation of how frequently they pass by a given area. The objective of this study was to describe spatial and temporal patterns of abundance of these four *Ctenus* species and to evaluate how army ants influence them.

METHODS

Study area.—The study was conducted in "Reserva Florestal Adolfo Ducke" (RFAD), 25 km North of Manaus, Amazon, Brazil. The reserve has 10,000 ha of "terra-firme" primary forest, over poor soils of tertiary origin (Chauvel, Lucas & Boulet 1987). Collections were made in an area of 2 × 5 km (Fig. 1). The northern half of this area is formed by plateaus, slopes and flat valley bottom of the stream "Barro Branco." In this area clay soils ("latossolo amarelo álico" or "aplic acrorthox") predominate, mainly in the plateaus and slopes, but there are sandy soils ("podzol
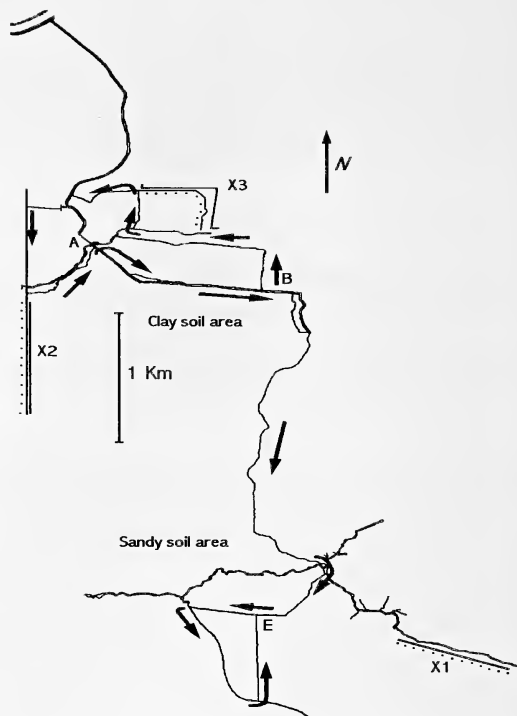
Figure 1.—Study area and the trails used in the extensive censuses. B = start and E = end of the main 12 km trail; arrows indicate the direction followed in this trail. "X1," "X2" and "X3" are additional trails. A = administration of the reserve.

álico" or "arenic tropaquod") in some of the lower parts of the slopes and in the valley bottom. Close to the streams the hydromorphic soils ("podzólicos vermelho-amarelo latossólicos" or "epiaquic paleudults") dominate. This area is covered by a dense forest called "Floresta de Terra-Firme" (in the restricted sense), except for the valley bottom, where the forest is dense, but lower, more humid and with more palms, a vegetation called "Floresta de Baixio" (descriptions in Guillaumet 1987). The southern half is the drainage basin of the stream "Acará." Clay soils are present on the more elevated areas next to the plateaus, but most of the work in the "Acará" valley was on sandy areas. The vegetation in this area is lower than the "terra-firme" forest on clay soils, and is generically called "Campinarana" (Guillaumet 1987). Next to the streams in the southern half there is also a predominance of hydromorphic soils. The temperature in the region of Manaus varies little annually, with a mean temperature of

25.8 °C in February and 27.9 °C in September (Salati et al. 1991). Mean annual rainfall in RFAD is 2480 mm, with a dry season from July–November (Marques-Filho et al. 1981). Data presented here were collected from November 1995 to March 1997.

Identification of spiders.—The size (measured as prosoma length) of adults varies among species: *C. manauara* (4–6 mm); *C. crulsi* (5.5–10.5 mm); *C. amphora* (5.5–11 mm); *C. villasboasi* (10–12.5 mm). Identification of spiders at species level is based mainly on reproductive structures (palp in male and epigynum in females), but inside RFAD all species of *Ctenus* are known, and the adults and larger juveniles can be identified based on color and design patterns on their body (descriptions and photographs in Höfer, Brescovit & Gasnier 1994). However, in the smaller juveniles the patterns of color and designs may be confused. During a preliminary phase of this study, we compared color and design patterns in juveniles of different sizes of the four species to provide criteria to distinguish the juveniles of each species in our study area. This was important because it allowed us to get much more data for the evaluation of abundance patterns. We present these criteria below. Vouchers were deposited in the aracnological collection of the Instituto Nacional de Pesquisas da Amazônia under the numbers INPA-001 to INPA-023.

On the back side of the opisthosoma of these *Ctenus* there is a white design similar to an amphora (Greek jar), generally followed by a series of triangles (a very similar pattern is also found in sympatric *Centroctenus*, which made us believe that this is a primitive characteristic for this and related genera). In the adults of *C. villasboasi* this design almost always disappears completely, but it is still visible in the smaller juveniles. *Ctenus villasboasi* can be identified after they reach 2–3 mm because the anterior part of the design is brighter and has the shape of the letter "U." Besides that, individuals larger than 5 mm have a distinct longitudinal white line on the ventral surface of the prosoma, unique in *C. villasboasi*. In *C. amphora* the triangles of the design almost always have disappeared completely in juveniles of size 3–4 mm, resulting in the typical amphora-shaped marking. Besides that, the pattern of coloration of the body, especially the ventral surface of the opisthosoma, is generally very dark.

Ctenus crulsi and *C. manauara* have the complete pattern of the design (amphora and triangles) from eclosion from the egg sac through the adult phase. Adults and subadults can be distinguished since adults of *C. manauara* are smaller than adults of *C. crulsi*, and the presence of the external copulatory organ (developed in adults or underdeveloped in subadults) is visible to the naked eye. Furthermore, they have some coloration differences, especially on the venter. Adults of *C. manauara* generally are brighter brown on the ventral surface, sometimes pink like the smaller juveniles of all species, and generally with a black spot near the spinnerets. The other species, including *C. crulsi*, have a large triangular design covering most of the ventral surface after they reach 3–4 mm. However, throughout the study, we found this pattern with ventral triangles on the opisthosoma also in adults of *C. manauara*, and possibly the ventral triangle may be delayed in appearing in the juveniles of *C. crulsi*. This means that we could have misidentified some juveniles of *C. manauara* as *C. crulsi* and *vice versa*. Therefore, we counted as identified only spiders larger than 4 mm, which was probably sufficient in avoiding misidentifications.

Censuses.—We captured spiders at night only, using rechargeable battery head lamps (Koehler Electric Cap Lamp). With these lamps the reflection of the light by the eyes of the spiders is visible up to 25 m, even for small individuals, but this depends on the position of the spider, the amount of litter and the density of the lower vegetation. Even when the position does not favor the reflection of the light, spiders may be localized by recognizing the spider's body or part of it.

In the censuses, the spiders were captured, identified, and immediately released at their capture site to minimize disturbance of the population. We employed two types of censuses: intensive censuses, for evaluation of temporal variation of the abundance of spiders, and extensive censuses, for evaluation of spatial patterns of abundance. In the intensive censuses we counted, at intervals of about two months, spiders in 10 small transects (each one of 60 × 1.5 m) per collection for a total of seven collections. The search was intensive, and we tried to capture all visible spiders

with prosoma length larger than 4 mm, which required 20 minutes to one hour per transect. Except for the first collection trip, the transects were in the same 10 defined areas, but in different positions inside the areas at each trip. With this procedure, we tried to include the variability inherent in the system and to obtain similar samples throughout the year, although not at exactly the same points. After the first sampling we realized that *C. crulsi* and *C. manauara* were nearly absent from all 9 selected areas, so we added an area, where individuals of these species were known to be abundant. An index to standardize the effort was applied to the abundance data for the first trip (abundance per species × 1.11), which compensates for one less transect, but this does not avoid an underestimation for the latter two species because this corrected mean still lacks the area where they are more abundant.

We identified and recorded the position of spiders on 15 km of trails in the extensive censuses, in June and October of 1995 and in February of 1996. Most of the trails constituted an almost continuous line of 12.5 km (Fig. 1), with small interruptions to avoid disturbed areas. The other three trails of about 1 km were outside this continuous line, but were included because they were the spatial extremes of the study area. These three trails are the last three segments in the graphical presentation of the abundance of spiders along the trails. The search for spiders was less intensive than in the previous census; and, depending on their abundance, we spent 30 minutes to two hours counting spiders in 1 km. The number of spiders found by this method was low per meter of transect, especially for small spiders, like juveniles and *C. manauara* (the smallest species), but the total number of spiders, even of *C. manauara*, was high.

The extensive censuses were used to show graphically how the abundance changed along these long transects and to calculate covariation indices among species. The trails were divided into segments of 100 m, which were our sample units. Data used to describe abundance graphically were the number of individuals of each species in each excursion per sample unit. We excluded from the covariation analyses sample units close to disturbed areas, and half of the sample units, avoiding contiguous segments of 100 m, to minimize

the dependency of the data. Data used for the evaluation of covariation were the sum of spiders in each sample unit in the three excursions. Based on the recapture rate of 100 marked adult spiders, we concluded that the sum of spiders per sample unit in three excursions was not biased by the fact that spiders could be counted more than once, because only 1% of the marked animals were found in one transect after one month. Soils type definition in the sample units consisted on a division first in hydromorphic and non-hydromorphic soils, and a division of the non-hydromorphic in clay and sandy soils. This categorization was rough, but sufficient for the analyses, as most places were inside one of the extremes of soil types. We used Pearson's index (Ludwig & Reynolds 1988) for the description of the interspecific covariation by pairs of species, excluding sample units where both elements of the pair were absent.

Estimating the frequency of raid occurrence of army ants.—We installed 40 pitfall traps, with a minimum distance between each of them of 200 m. Each trap consisted of a plastic container (diameter of opening 8 cm, 20 cm deep) buried flush with the surface, and an aluminum cover 10 cm above the trap for protection against rain, not obstructing the entrance of invertebrates. We used picric acid inside the trap as a preservative liquid. Two samples were made for periods of 90 days, from March–June 1995, and from October–February 1996. The samples were preserved in 70% alcohol. We counted the number of army ants of the species *Eciton burchelli* and *Labidus predator*, which are the swarm-raiding species that attack *Ctenus*. Considering that a spider could be where a trap was, we used the proportion of traps with more than 10 army ants of the same species (a probable raid), as an index of frequency of risky encounters for *Ctenus*.

RESULTS

We recorded 494 individuals of *Ctenus* during seven excursions with intensive censuses and 1304 individuals during three extensive censuses. The abundance of *Ctenus amphora* and *C. villasboasi* was high in December 1994, gradually decreased until July, and increased again after August (Fig. 2), suggesting seasonal variation. The abundance of *Ctenus manauara* was also low during the dry season.
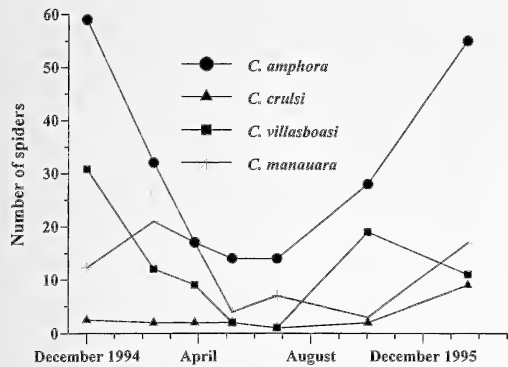
Figure 2.—Number of individuals per species collected in the intensive censuses throughout one year.

Because the census value for December 1994 was probably underestimated (see methods), it is reasonable to assume that it followed the same pattern of the above species. Data from intensive censuses, which was used to describe the patterns above, were not enough to evaluate temporal variation for *C. crulsi*. However, the totals of *C. crulsi* counted in the three extensive censuses in July, October and February 1995 were respectively 63, 129 and 191, a similar temporal variation compared to *C. amphora*, 77, 171 and 235, which means that all species have similar temporal patterns of abundance—or at least that they do not differ strongly.

Comparing the abundance between pairs of species per sample unit, we found significant negative covariation only in the pairs *C. amphora* × *C. crulsi* and *C. amphora* × *C. manauara* (Table 1). The comparison of spatial patterns of abundance (Fig. 3) facilitated the interpretation of these negative correlations. There were large areas with dominance of *C.*

amphora where *C. crulsi* and *C. manauara* had low abundance, and *vice versa*. Although the abundances of *C. crulsi* and *C. manauara* were not positively correlated, the comparisons revealed very similar spatial patterns of abundance. Apparently, covariance analysis was not appropriate to evaluate patterns of abundance in this case because the number of individuals per sampling unit was low and because there were many points where both species of the pair were absent. There were three consistent large scale spatial patterns of abundance: *C. amphora* had the highest densities between positions 80 and 150; *C. crulsi* and *C. manauara* had the highest densities between 1–80 and between 150–180; and *C. villasboasi* had a relatively homogeneous distribution.

The total abundance varied through time, but the spatial patterns of abundance within each species were very similar in the three censuses. The positions 80–150, where *C. amphora* was more abundant, were mostly on sandy (55%) or hydromorphic (38%) soils, while the positions 1–80 and 150–180, where *C. crulsi* and *C. manauara* were more abundant, were mostly on clay (64%) or hydromorphic (27%) soils. There are two pieces of evidence suggesting that soils could, directly or indirectly, determinate which species dominates an area: a) the change in dominance from *C. crulsi* and *C. manauara* to *C. amphora* between positions 70 and 90 was coincident with a change in predominant soil from clay to sandy; b) *C. crulsi* and *C. manauara* were almost absent in a large area of white sandy soils, but both appeared in two censuses inside this area, in the only place with a small segment of about 500 m of intermediate sandy-clay soil in the trail.

Table 1.—Interspecific covariation between pairs of *Ctenus* species. Pearson = Pearson's correlation coefficient after excluding sample units where both species in the pair were absent; P = probability associated to the correlation; n = sample size; Sign = significance calculated considering 6 tests: * = significant, ns = non significant.

Pairs of species	Pearson	P	n	Sign
C. amphora × *C. crulsi*	−0.48	<0.001	67	*
C. amphora × *C. manauara*	−0.34	0.006	64	*
C. amphora × *C. villasboasi*	0.00	0.99	62	ns
C. crulsi × *C. manauara*	0.02	0.91	49	ns
C. crulsi × *C. villasboasi*	−0.23	0.07	61	ns
C. manauara × *C. villasboasi*	−0.26	0.05	57	ns
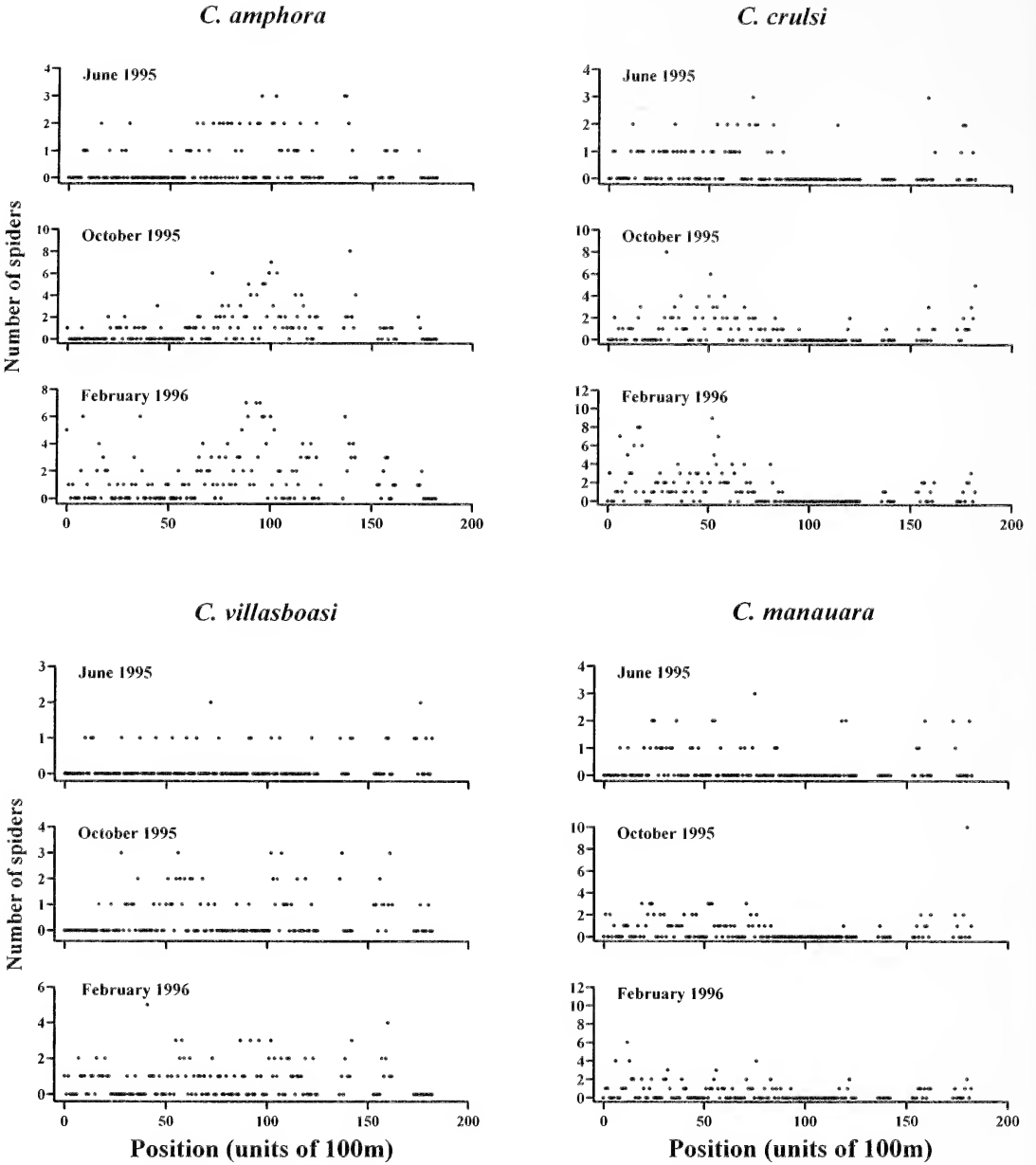
Figure 3.—Number of individuals collected along the extensive censuses trails for each species in three periods. Three patterns of abundance were detected: one for *Ctenus amphora*, one for *Ctenus crulsi* and *Ctenus manauara*, and one for *Ctenus villasboasi*.

Considering these differences in relation to soils, we calculated two indices of frequency of risky encounters with army ants, one for clay soil areas and another for sandy soil areas. The traps in hydromorphic soils areas were in insufficient number to be included in the analysis. The proportion of traps with army ants and the amount of army ants were higher in the clay soil areas (Table 2). Clay soil areas had a much higher index of risk of encounters with army ants (0.92) than sandy soil areas (0.21). We suppose that life span for *Ctenus* is between 6–12 months; therefore, it is highly probable that every *Ctenus* individual encounters army ants at least once during its life in clay soils, while many *Ctenus* will

Table 2.—Number of pitfall traps with different amounts of army ants in sandy and clay soils in two periods of the year.

Soil	Absence of ants	1–10 ants	10–100 ants	>100 ants
April–June 1995				
Clay	1	1	2	7
Sandy	1	2	1	1
December 1995–February 1996				
Clay	0	0	8	7
Sandy	3	5	1	0

probably never encounter army ants on sandy soils.

DISCUSSION

The four *Ctenus* species are sympatric throughout the study area. However, there were strong differences in the spatial patterns of abundance of the species, which were stable during the study. Although the amount of spiders changed throughout the year, the general pattern of locational dominance remained. The predominant species in a given place is probably determined by local characteristics of the environment, which favor one species more than the other. However, it is not clear what these environmental characteristics are, and why the favored species in a given place do not exclude the others.

Based on our data, we can conclude that army ants are important predators of *Ctenus*, but a more detailed study would be necessary to determinate if they are a key factor that facilitates coexistence in this system. One evidence that the ants may be important for coexistence is that on clay soils, where army ants are more abundant, the four species are relatively common. However, predation alone would not explain why the dominant species is not the same all over the area.

The temporal variation in the abundance of spiders probably reflected seasonal variation of the environment. Evidence of seasonal variation in the abundance of ctenid-pisaurid spiders was not detected by Gasnier et al. (1995) in this forest; however, this was observed in a year with less pronounced seasons. The cause of variation in the present study is not clear, there are many possible reasons, e.g., a seasonal variation of the amount of leaf litter could restrict the amount of refuges or prey

available, or the absence or excess of rain could cause a seasonal variation in mortality. Whatever the cause, seasonality may facilitate the coexistence of species either by maintaining the species under a level in which their interactions would influence coexistence or by differentiation in seasonal peaks of activity or abundance. Sympatric species of forest-floor spiders may differ by seasonal peaks of abundance (Niemelä et al. 1994), but we did not find this difference among the *Ctenus* species. For a further discussion on how seasonality could affect coexistence in this system it will be necessary to evaluate the mechanism by which environmental seasonality affects the abundance of these spiders.

Evaluations of spatial patterns of abundance or distribution (e.g., Cutler & Jennings 1992; Fernandez-Montraveta, Lahoz-Beltra & Ortega 1991; Greenstone 1979, 1980) are not frequent in the spider literature. Authors defending the use of an experimental approach as the safer mode to evaluate coexistence of species recognize the importance of basic knowledge (e.g., spatial patterns of abundance) to plan and interpret the experiments (e.g., Hairston 1989; Wise 1993). However, there is little discussion on the procedures of how to build this knowledge. The use of interspecific covariation is one of the standard forms to detect patterns of coexistence (Ludwig & Reynolds 1988). However, in our study, the evaluation by interspecific covariation did not show any evidence for the similar patterns of abundance of *C. crulsi* and *C. manauara*. We recommend the interpretation of the indices of covariation in conjunction with an evaluation of spatial patterns of abundance. Evaluations based on graphics of abundance along transects (or on bidimensional maps of abundance) may help to detect important factors that affect a species, especially if the repetition of the censuses indicates that the pattern is stable in time, which probably reflects a local factor. After the pattern is established, and considering the dimension of the areas of higher abundance, the researcher may go back to the field and consider potential factors affecting the abundance. During the comparison of spatial patterns of abundance among species by superposition of graphs unexpected differences may arise, which makes this a powerful tool in the development of hypothesis for the abundance and coexistence of species.

ACKNOWLEDGMENTS

LITERATURE CITED

Chauvel, A., Y. Lucas & R. Boulet. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experientia 43: 234–241.

Cutler, B. & D.T. Jennings. 1992. Habitat segregation by species of *Metaphidippus* (Araneae: Salticidae) in Minnesota. Journal of Arachnology 20:88–93.

Edgar, W.D. 1971a. Seasonal weight changes, age structure, natality and mortality in the wolf spider *Pardosa lugrubis* Walck. in Central Scotland. Oikos 22:84–92.

Edgar, W.D. 1971b. Aspects of the ecological energetics of the wolf spider *Pardosa (Lycosa) lugubris* (Walckeanaer). Oecologia 7:136–54.

Fernandez-Montraveta, C., R. Lahoz-Beltra & J. Ortega. 1991. Spatial distribution of *Lycosa tarentula fasciiventris* (Araneae, Lycosidae) in a population from central Spain. Journal of Arachnology 19:73–79.

Ford, M.J. 1977. Metabolic cost of the predation strategy of the spider *Pardosa amentata* (Clerck) (Lycosidae). Oecologia 28:333–340.

Ford, M.J. 1978. Locomotory activity and the predation strategy of the wolf spider *Pardosa amen-*

tata (Clerck) (Lycosidae). Animal Behaviour 26: 31–35.

Gasnier, T.R., H. Höfer & A.D. Brescovit. 1995. Factors affecting the activity density of spiders on tree trunks in an Amazonian rainforest. Ecotropica 1:69–77.

Greenstone, M.H. 1978. The numerical response to prey availability of *Pardosa ramulosa* (McCook) (Araneae: Lycosidae) and its relationships to the role of spiders in the balance of nature. Symposia of the Zoological Society of London 42:189–93.

Greenstone, M.H. 1979. A line transect density index for wolf spiders (*Pardosa* spp.), and a note on the applicability of catch per unit effort methods to entomological studies. Ecological Entomology 4:23–29.

Greenstone, M.H. 1980. Contiguous allotopy of *Pardosa ramulosa* and *Pardosa tuoba* (Araneae: Lycosidae) in San Francisco Bay Region, and its implication for the patterns of resource partitioning in the genus. American Midland Naturalist 104:305–311.

Guillaumet, J.-L. 1987. Some structural and floristic aspects of the forest. Experientia 43:241–251.

Hairston, N.G. 1989. Ecological Experiments: Purpose, Design, and Execution. Cambridge Univ., Cambridge.

Hallander, H. 1970a. Environments of the wolf spider *Pardosa chelata* (O.F. Mühller) and *Pardosa Pullata* (Clerk). Ekologia Polska 18:41–72.

Hallander, H. 1970b. Prey cannibalism and microhabitat selection in the wolf spiders *Pardosa chelata* O.F. Mühller and *P. pullata* Clerck. Oikos 21:337–340.

Höfer, H., A.D. Brescovit & T. Gasnier. 1994. The wandering spiders of the genus *Ctenus* (Ctenidae, Araneae) of Reserva Ducke, a rainforest reserve in central Amazonia. Andrias 13:81–98.

Ludwig, J.A. & J.F. Reynolds. 1988. Statistical Ecology. A Primer on Methods and Computing. Willey & Sons. New York.

Marques-Filho, A.O., M.N.G. Ribeiro, H.M. dos Santos, J.M. dos Santos. 1981. Estudos climatológicos da Reserva Florestal Ducke. IV. Precipitação. Acta Amazônica 11:759–768. Manaus.

Niemelä, J., T. Pajunen, Y. Haila, P. Punttila & E. Halme. 1994. Seasonal activity of boreal forest-floor spiders (Araneae). Journal of Arachnology 22:23–31.

Salati, E., M.N.G. Ribeiro, M.L. Absy & B.W. Nelson. 1991. Clima da Amazônia: Presente, Passado e Futuro. Pp. 21–34, *In* Bases Científicas para Estratégias de Preservação e Desenvolvimento da Amazônia: Fatos e Perspectivas, Vol 1. (A.L. Val , R. Figliuolo & E. Feldberg, eds.) Instituto Nacional de Pesquisas da Amazônia, Manaus.

Schmitt, A., M. Schuster & F.G. Barth. 1990. Daily

locomotor activity patterns in three species of *Cupiennius* (Araneae, Ctenidae): The males are the wandering spiders. Journal of Arachnology 18:249–255.

Schuster, M., D. Baurecht, E. Mitter, A. Schmitt & F. Barth. 1994. Field observations on the population structure of three ctenid spider (*Cupiennius*, Araneae, Ctenidae). Journal of Arachnology 22:32–38.

Suwa, M. 1986. Space partitioning among the wolf spider *Pardosa amentata* species group in Hokkaido. Japanese Research in Population Ecology 28:231–252.

Van Dyke, D. & D. Lowrie. 1975. Comparative life histories of the wolf spider *Pardosa ramulosa*

and *P. sierra* (Araneae: Lycosidae). Southwestern Naturalist 20:29–44.

Vieira, R.S. & H. Höfer. 1994. Prey spectrum of two army ant species in central Amazonia, with special attention on their effect on spider populations. Andrias 13:189–198.

Vieira, R.S. & H. Höfer. 1998. Efeito do forrageamento de *Eciton burchelli* (Hymenoptera, Formicidae) sobre a araneofauna de liteira em uma floresta tropical de terra-firme na Amazônia Central. Acta Amazonica 28:345–351.

Wise, H.D. 1993. Spiders in Ecological Webs. Cambridge Univ., Cambridge.

ONTOGENETIC CHANGE IN COLORATION AND WEB-BUILDING BEHAVIOR IN THE TROPICAL SPIDER *ERIOPHORA FULIGINEA* (ARANEAE, ARANEIDAE)

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ABSTRACT. *Eriophora fuliginea* (Araneae, Araneidae), a tropical orb-weaving spider from Panama, undergoes a dramatic color change in the course of its ontogenesis. The first free instar has an amber opisthosoma, which soon becomes bright yellow, later green. Subadults change to olive, adults are dark brown with a white median stripe. Parallel to this color modification the spider's behavior changes as well. The main activity phase shifts from day to night and web architecture changes from symmetrical horizontal orb-webs on the upper side of leaves with the spider on the hub, to asymmetrical horizontal orb-webs between shrubs with spiders in a rolled leaf nearby.

Keywords: Ontogenetic change, development, coloration, behavior, orb web

Quite often in the field, particularly in the tropics, one encounters colorful, juvenile spiders. When kept in the laboratory in many cases they change their coloration, frequently in a species-specific ontogenetic sequence. Since juvenile spiders normally cannot be identified, such coloration changes usually are not well documented, but may be very common. Only a few cases have been reported in the literature. The European sparassid spider *Micrommata virescens* (Clerck 1757) is an example of a spider of temperate regions where the males change from light green, to yellow, to greenish-yellow with red stripes or dots (Homann 1946). Bonnet (1929, 1930) describes the distinctive changes in color and pattern in *Nephila madagascariensis* (Vinson 1868). Edmunds & Edmunds (1986) report on two araneid species that show a distinct ontogenetic color change. *Araneus rufipalpis* (Lucas 1858) changes its color from a juvenile bright green, to a greyish-green or greyish-brown, to an adult dark brown. In *Gasteracantha curvispina* (Guérin 1837), the juvenile spiders are flecked white and brown, whereas the adults are white, yellow, orange, brown, red, or even striped in light and dark colors.

Different coloration of juveniles and adults within one species could indicate that different instars use different niches to reduce intraspecific competition. Such avoidance of competition between adults and their own off-spring would be reasonable (e.g., Begon et al. 1996) and could include selection of different habitats, diurnal activities or food. An ontogenetic color change would support such important changes in a spider's life, but reports on the coincidence of color change and niche use are rare.

During an investigation on the prey composition of large orb-weaving spiders (Nentwig 1985), unknown small green juvenile spiders encountered during field research in Panama developed in the laboratory into dark brown adult spiders and were later identified as *Eriophora fuliginea* (C.L. Koch 1839) (Araneae, Araneidae). Later, dark brown females of the same species were caught in the field and built a cocoon in the laboratory from which amber juvenile spiders emerged. A sequence of the differently colored developmental stages was described in clutches of two females and was correlated to changes in the behavior that the juvenile spiders underwent as they matured.

METHODS

Two adult female *E. fuliginea* were caught in Panama (Parque Nacional Soberania, Gamboa) and brought to our laboratory. They were kept in cages (32 × 35 × 10 cm) made of wood and wire in a climate chamber (25–30 °C, 40–50% RH, L:D = 16:8 h), where they built one cocoon each on days 6 and 9 after

capture. After 29–32 days, the juvenile spiders hatched from the cocoons. The spiderlings (n = 200) were kept individually in transparent plastic boxes with lids (20 × 20 × 8.5 cm) which were set up on edge within a climate chamber (25–30 °C, 40–50% RH, L:D = 12.5:11.5 h). The bottom of each box was covered with plaster, which was kept damp to ensure a humidity within the boxes of approximately 100%. A cotton thread was attached to the inside of each box to provide fixing points for webbuilding. Flies of various species (*Drosophila melanogaster, Musca domestica, Calliphora erythrocephala, Protophormia terraenovae*) were provided *ad libitum* as food, with the fly size dependent on spider size. Due to high mortality especially in instars III and IV (days 20–40) and due to killing spiders for section preparations, only 40 spiders became adult.

The coloration and pattern of the growing spiders were recorded, sketched and photographed from hatching until their death as adult animals. The bases for the colorations and patterns were observed on live animals, on preparations of animals freshly killed with CO_2, and on sections. For each main color form, the opisthosoma of 2–3 freshly killed spiders were fixed in parts in 2% osmium tetroxide in potassium dichromate buffer according to Dalton (Glauert 1974). The preparations were then studied with the optical or electron microscope for the position of pigment granula. A white coloration is caused by guanine crystals which are deposited in guanocytes and can easily be recognized by the aid of Holl (1987). Yellow, red and brown colors are caused by different ommochromes, which are stored intracellurlarly as membrane-shielded granules. Green colors usually derive from linear tetrapyrroles (Holl 1987). No attempt was made to further identify the chemical basis of the colors.

Apart from recording the web building behavior with a video camera (one frame per second; night recordings with a lens sensitive to red light), the spiders were observed individually during the day, and at three different development stages during the night (22 animals on day 52 after hatching, 18 animals on day 90 and 16 adult animals on day 125). The observed activities were logged according to type and duration. The orb-webs were analyzed for differences between juvenile and adult pattern, especially orb web symmetry and position of the spider in hub or retreat. Voucher specimens are deposited in the Natural History Museum, Basle, Switzerland.

RESULTS

Coloration and pattern.—The opisthosoma of freshly emerged juvenile spiders is amber, with three large and one small pair of black, slightly curved abdominal stripes on the dorsal side (Fig. 1). The diffuse deposition of guanine in the dorsal integument that begins frontally at approximately day 10 after hatching continues until the guanine is condensed to a tight layer between days 20–40 and causes a general lightening of the color. Parallel to this the opisthosoma turns from amber to bright yellow between days 15–60. The pattern expands with a fifth pair of abdominal stripes appearing with the second molting, two to three black median dots (small elevations in the cuticle filled with black pigments) and a posterior line. Simultaneously with the deposition of guanine, dark brown pigments begin to accumulate frontally on the opisthosoma, solidifying in the course of the next color change into a black band encircling the opisthosoma latero-dorsally (Fig. 2).

In most cases a shift from yellow towards green occurs at this time, which can be more-or-less pronounced: a) the color change either begins between the rear abdominal stripes and expands forwards, leaving the entire width of the frontal opisthosoma yellow and giving the entire opisthosoma a greenish-yellow cast, or b) the whole dorsal opisthosoma changes color, giving it a more yellowish-green cast before darkening to green (Fig. 7). The first variation can be found between days 17–67, the second between days 36–59.

The next color change initiates a darkening of the coloration. A longitudinally oriented V appears, which is first light brown in color, but darkens increasingly. As a result the dorsum becomes divided into a rostral and a caudal area. Based on the preceding color variation, different patterns ensue (Fig. 3): a) a tri-colored variation with a yellow area in front of, and a green area behind, the brown V, or b) a bi-colored variation with the brown V in the middle of the uniformly green opisthosoma. Male *E. fuliginea* show these variations between days 50–63, females between days 50–80 (Fig. 7).
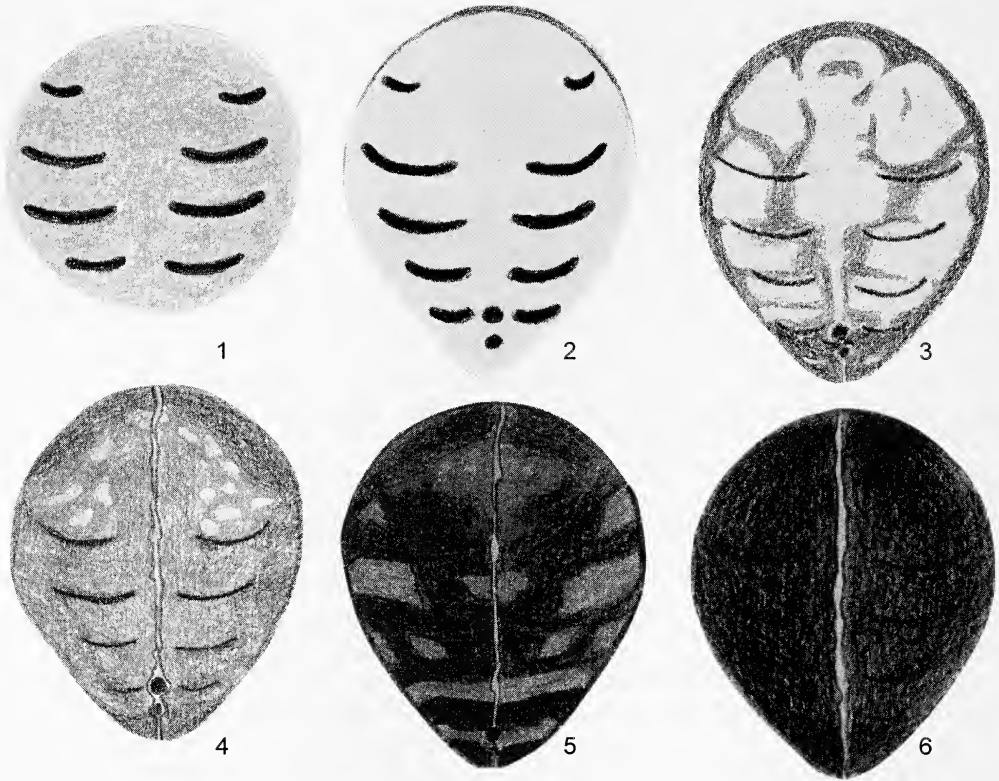
Figures 1–6.—Color pattern of the dorsal opisthosoma of *Eriophora fuliginea*. 1. Instar I II; 2. Instar II-V; 3. Instar V-VII; 4. Instar VII (male), instar VII-VIII (female); 5. male, instar VIII-IX (adult); 6. Female, instar VIII-X (adult). Since color changes continuously irrespective of molting, the indication of instars is only approximative. *Scale:* Opisthosoma length of instar I is about 1 mm, adult females 15–25 mm. The colored version of these figures can be found at http://www.cx.unibe.ch/zos/syn.htm (go to publications, 2001).

As the V gets darker the abdominal stripes lose definition and blend into the pattern, changing color from black to a dark reddish-brown. Between the two legs of the V an off-white median stripe begins to form. In all color variations the areas in front of and behind the V change color in such a way that they appear olive-colored with either a yellowish, greenish or brownish cast. The anterior area tends to show a pattern of yellow and brownish-olive flecks, while the posterior area begins to display stripes of olive and brown. These variations appear in females between days 69–99 and in males between days 60–80 (Figs. 4, 7).

Between days 80–120 (females) and days 72–195 (males) the color shifts toward brown. In the males, the dark pattern of the dark brown V expands after approximately day 101, particularly towards the front, decreasing

the lighter area (lighter spots on medium dark brown). The contrast in the stripes becomes more pronounced with light (light brown or light greyish-brown) and dark (dark brown or brownish-black) stripes alternating. Additionally, short light hairs grow on the lighter stripes and short dark hairs grow on the darker stripes (Fig. 5).

In females, the V expands forwards as well, but less distinctly than in the males because of its lighter color. The anterior area stays lighter longer, sometimes flecked or mottled yellow or whitish on brown. The stripes in the posterior part shift towards brown and become less distinct. Most females develop a uniform dark brown to brownish-black coloration after this until the opisthosoma is only marked with a whitish median stripe (Fig. 6).

In both females and males the abdominal stripes turn a more reddish-brown during the
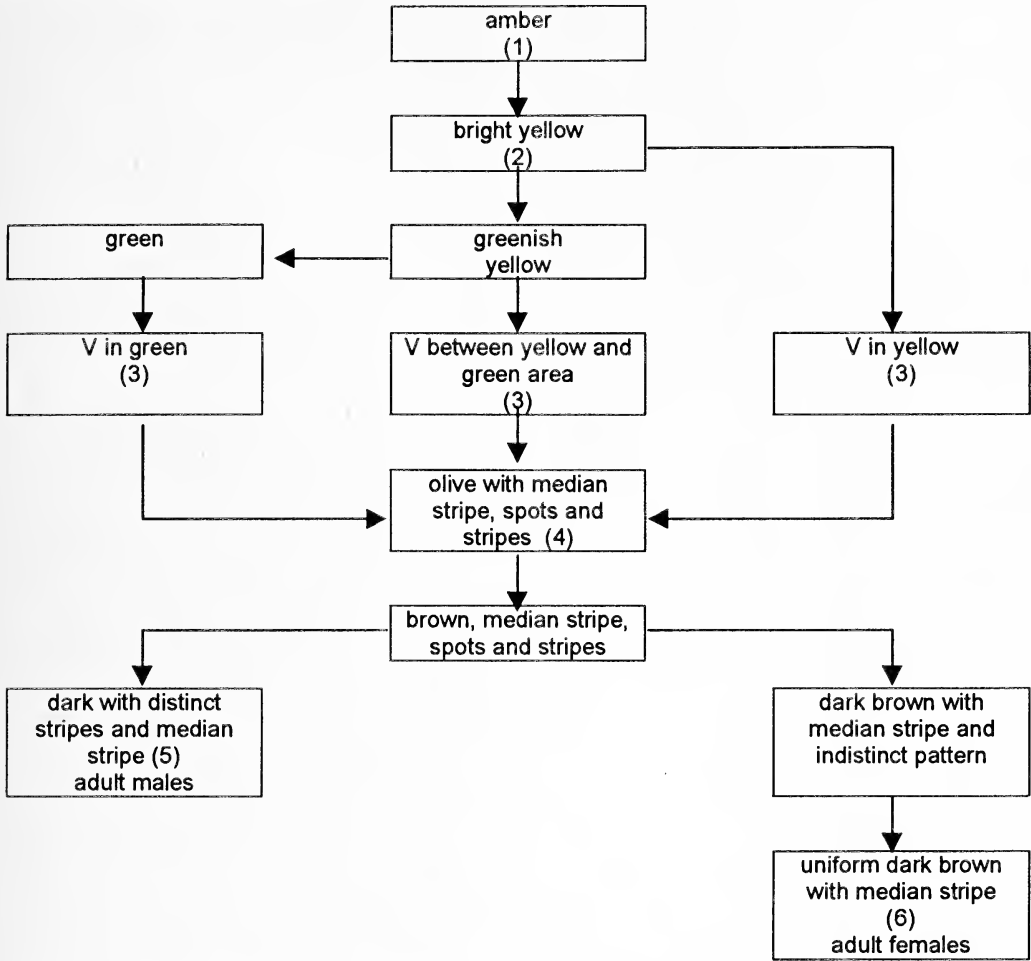
Figure 7.—Sequence of color changes in the dorsal opisthosoma of *Eriophora fuliginea*. Numbers refer to Figs. 1–6.

last two or three color changes, becoming thinner and less distinct, until they are only recognizable as hairless borders in adult females. The caudal median black spots are found in all animals except in adult females where they dissolve. In addition to these patterns many animals show variations in color, spots and stripes which we consider to be individual modifications.

Color origin.—The various colors of *E. fuliginea* have different origins. The amber color, particularly of the juvenile spiders, is based on the transparent coloration of the cuticle. With increasing thickness of the cuticle the amber becomes darker (dark amber to reddish-brown), e.g., in the prosoma of older animals, where the cuticle is very solid. Thinner cuticle can be grey to greyish-brown, e.g., in

the dorsal opisthosoma of older animals. It was not possible to judge how far this is a true coloration of the cuticle.

The yellow color originates either in the cuticle or in the hypodermis. It was impossible to locate accurately as the yellow color dissolves quickly in 70% alcohol. All that can be seen in the light microscope in individuals with a yellow opisthosoma is a hypodermis poor in dark pigments. The green color, the reddish-brown color of the abdominal stripes as well as the brown and dark brown colors of the opisthosoma-encircling band, the V, the stripes of the pattern and the adult coloration of the females are based in the hypodermis.

The guanine stored in guanocytes provides a white background that causes the colors to be opaque, rather than transparent, and bright

as in the case of the yellow, yellowish-green and green-colored animals. The guanine is not distributed evenly over the opisthosoma. The lateral and dorsolateral guanocytes differ in their guanine content, creating the striped pattern. The opisthosoma's median stripe is caused by the dorsomedian guanocytes, which contain large deposits of guanine, and by the low density of dark pigments in the hypodermis of this area.

Web building behavior.—The spectrum of activities observed in *E. fuliginea* includes walking, construction and destruction of orb-webs, perching in the hub, construction of a hiding place and hiding, catching and eating prey, as well as molting. Although all development stages of *E. fuliginea* show these activities, differences can be found in manner, frequency and timing. Walking constitutes the major part of the moving activities of all age groups. Juvenile spiders were observed walking in short bouts of up to 5 min during the day until day 60, juvenile and adult spiders in bouts from few min to over 1 h during the night.

Juvenile *E. fuliginea* begin orb-web building on day 9 or 10. Up until day 47 they build webs only every second or third day, mostly during the day. Webs of juveniles are small and very variable in form and spatial arrangement, either as horizontal orbs or as orbs which are not plane, thus resembling three-dimensional webs. Older animals shift their web building activities to the night and build bigger, mostly two-dimensional, and more and more asymmetric webs, with the hub being placed near the upper end of the web and the lower capture area being enlarged. Destruction of the webs was observed towards the end of the night. *Eriophora fuliginea* spends 30–70% of its time sitting in the hub of its web. With increasing age, however, fewer individuals are observed sitting on the web during the day: Up to day 60 the yellow and green spiders sit 30–40% of the time in the hub; after day 90 the dark brown spiders spend less then 10% of their time in the hub.

DISCUSSION

Types of color change.—In *E. fuliginea*, the changes in color occur gradually and independently of molting. They are irreversible color changes, not temporary, reversible adaptations to varying backgrounds as can be the case in species that undergo rapid color changes after disturbances. Examples of reversible color change are *Phonognatha graeffei* (Keyserling 1865) (see Roberts 1936), *Cyrtophora cicatrosa* (Stoliczka 1869) (see Blanke 1975) and *Argiope flavipalpis* (Lucas 1858) (see Edmunds & Edmunds 1986). These species react to disturbances by dropping to the ground and changing from a dark color with a distinctly striped white pattern to a darker, indistinctly patterned color within fractions of a second, thus blending into the background.

This rapid color change is usually based on the contraction of guanocytes (Blanke 1975; Holl 1987) which diminishes the dimension of the white areas. The original color is usually re-established in less than 1 h. Contrary to this rapid and reversible so-called physiological color change (Holl 1987) examples are known of a different reversible color change that takes place slowly and results in different color varieties. This morphological color change (Aechter 1955) is found in animals that adapt their color to their environment once or several times in their lives. One of the best known examples of this slow color change are the crab spiders. The females of *Misumena vatia* (Clerck 1757) can slowly but reversibly adapt their body color to a white or yellow background. Individuals of the araneid *Cyrtophora citricola* (Forskal 1775) can adapt their color to a new environment over the course of 2–4 wk.

In our study, the juveniles of *E. fuliginea* were observed to be much more frequent in the green color variation in the field than in the laboratory. The varying degrees of the shift from yellow to green at this stage found in the juvenile spiders raised in the laboratory might represent adaptations to the background which are not reversible *per se*, but lose most of their distinctiveness in the final adult color. Experiments with individuals being raised on different backgrounds might provide insights into this phenomenon.

Holl (1987) lists a third type of color change apart from the physiological and the morphological kind, a so-called ontogenetic color change. The resulting coloration is irreversible. According to Holl, it appears to be associated with metamorphosis or molting in arthropods. Since the color change in *E. fuliginea* progresses continuously and indepen-

dently from the molts, it does not conform totally to Holl's definition. Since ontogenetic implies, however, that the color change occurs parallel to the ontogenesis of an animal we feel that the color change of *E. fuliginea* can be classified as such.

Different explanations can be considered for the function or purpose of the various colorations and patterns of *E. fuliginea*. It is rather unlikely that any of the colorations play a role in the thermoregulation of *E. fuliginea* although that function has been reported for *Argiope argentata* (Fabricius 1775) (see Robinson & Robinson 1978). The opisthosoma of *A. argentata*, a spider that is exposed to the sun as it sits in its orb-web during the day, is colored silvery-white in large areas, reflecting the sunlight and thus reducing the thermal effect of this exposure. The yellow forms of *E. fuliginea*, being the lightest color variation of the different forms and therefore possibly playing a similar role as the silvery-white coloration of *A. argentata*, are hardly ever exposed to the sun in their natural habitat. More often, the various colorations and patterns confer a different kind of protection on their bearers. Many species signal to others their dangerousness and/or inedibility by their aposematic colors.

Function of color change.—*Eriophora fuliginea*, however, belongs to the group of animals that render themselves invisible to their prey as well as to their enemies through their coloration and behavior. The most widely spread strategy for chromatic camouflage is an adaptation to the background. Juvenile *E. fuliginea* sport colors that are found frequently in the vegetation: amber (light orange-brown), yellow, green. A successful camouflage in front of a like-colored background is easily imaginable. Examples are the diverse color variations of the crab spiders with white, yellow, green and even red coloring, depending on their host plant. In Panama, *E. fuliginea* was often observed on the hub of its horizontal orb-web constructed on the upper side of leaves during this "plant-colored" phase. The yellow color of the juvenile spiders might have the additional effect of rendering them invisible to UV-sensitive (and thus red-blind) prey, as is the case in *Misumena vatia* (see Hinton 1976). It is likely that the more contrastingly colored forms of *E. fuliginea* do not expose themselves on leaves, at least not in the bright daylight. The results of the laboratory observations support this assumption, as a shifting of the activities into the night was observed parallel to this color change. The spotted, mottled and striped patterns of *E. fuliginea* are similar to those of other spiders. Many araneids have developed such outline-dissolving patterns (Robinson & Robinson 1978). This is especially important for species that do not sit directly in front of their backgrounds, as a purely chromatic adaptation would not suffice for camouflage in this case (Robinson & Robinson 1970). According to observations in the field, adult *E. fuliginea* construct their large vertical orb-webs more and more between bushes with advancing age and therefore are further removed from the background than the juvenile spiders that construct their webs between or on leaves. As the potential predators of *E. fuliginea*, like nocturnal lizards, small primates and insectivores, possess much better night vision than humans, this reasoning is still valid in the face of the shift of the activities into the night.

Concluding, the main function of the changing coloration of *E. fuliginea* is likely to be to camouflage the spider adequately during the two different phases of its life. In the juvenile part, spiders are primarily yellow to green, diurnal, and build small symmetric orb webs in large leaves. In the second life part, spiders change to dark brown, are more nocturnal, and build large asymmetric orb webs in vegetation gaps.

ACKNOWLEDGMENTS

LITERATURE CITED

Aechter, R. 1955. Untersuchungen über die Zeichnung und Färbung der Araneen unter Berück-sichtigung der Ontogenie und Phylogenie. Sitzungberichte Österreichische Akademie der Wissenschaften Mathematisch-Naturwissenschaften und Erdwissenschaften I 164:545–606.

Begon, M., J.L. Harper & C.R. Townsend. 1996. Ecology. Blackwall, Oxford.

Blanke, R. 1975. Die Bedeutung der Guanozyten für den physiologischen Farbwechsel bei *Cyrto-*

phora cicatrosa (Araneae: Araneidae). Entomologia Germanica 2:1–6.

Bonnet, P. 1929. Les araignées exotiques en Europe; II. Elevage à Toulouse de la grande araignée fileuse de Madagascar et consideration sur l'Aranéiculture (première partie). Bulletin de la Societe Zoologique de France 54:501–523.

Bonnet, P. 1930. Les araignées exotiques en Europe; II. Elevage à Toulouse de la grande araignée fileuse de Madagascar et consideration sur l'Aranéiculture (seconde partie). Bulletin de la Societe Zoologique de France 55:53–77.

Edmunds, J. & M. Edmunds. 1986. The defense mechanism of orb weavers (Araneae: Araneidae) in Ghana, West Africa. Pp. 73–89. *In* Proceedings of the Ninth International Congress of Arachnology. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, ed.). Panama 1983, Smithsonian Institution.

Glauert, A.M. 1974. Fixation, dehydration and embedding of biological specimens. Pp. 1–207. *In* Practical Methods In Electron Microscopy 3 (A.M. Glauert, ed.). North Holland/American Elsevier, Amsterdam.

Hinton, G.E. 1976. Possible significance of the red patches of the female crab-spider *Misumena vatia*. Journal of Zoology (London) 180:35–39.

Holl, A. 1987. Coloration and chromes. Pp. 16–25. *In* Ecophysiology of Spiders. (W. Nentwig, ed.) Springer, Berlin.

Homann, H. 1946. Über die Jugendform von *Micrommata viridissima* (Deg.) (Araneae). Biologisches Zentralblatt 65:82–83.

Nentwig, W. 1985. Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. Oecologia 66:580–594.

Roberts, N.L. 1936. Color change in the leaf-curling spider (*Araneus wagneri*). Proceedings of the Royal Zoological Society of New south Wales 28–29.

Robinson M.H. & B.C. Robinson. 1970. The stabilimentum of the orb-web spider *Argiope argentata* (Araneae: Araneidae): An improbable defense against predators. Canadian Entomologist 102:641–655.

Robinson, M.H. & B.C. Robinson. 1978. Thermoregulation in orb-web spiders: New descriptions of thermoregulatory postures and experiments on the effects of the posture and coloration. Zoological Journal of the Linnean Society 64:87–102.

SHORT COMMUNICATION

ZOROPSIDAE: A SPIDER FAMILY NEWLY INTRODUCED TO THE USA (ARANEAE, ENTELEGYNAE, LYCOSOIDEA)

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ABSTRACT.   The spider family Zoropsidae is newly recorded for the USA, bringing the total to 68 families. *Zoropsis spinimana* (Dufour 1820), native to the Mediterranean region, has been established in the San Francisco Bay area since at least 1995. The identification and phylogenetic position of this species are provided.

Keywords: Spiders, exotic, introduction, Zoropsidae, Lycosoidea

Zoropsis spinimana (Dufour 1820) has been encountered several times over the past five years in the San Francisco Bay region of California. This remarkable species was first brought to the attention of Marge Moody of the California State Department of Agriculture (CDFA) who sent specimens to us at the California Academy of Sciences (CAS) for identification. An additional specimen was sent to us by Rick Vetter of the University of California, Riverside (UCR). Both males and females have been encountered, and specimens have been taken both in houses and in nurseries. Records are from the winter and spring (December through May) and early fall (September and October). The presence of this species in at least five cities in two counties suggests that *Zoropsis spinimana* (Dufour) has been introduced to and established in the San Francisco Bay area of central California. According to one informant, the spiders were found "high on interior walls or ceilings." A captive female made no web for prey capture. When that female produced an egg sac in April she surrounded the sac with a wall of cribellate silk; cribellate silk was carded with mobile leg IV (Eberhard & Pereira 1993). Captive spiders were not aggressive and may not be considered dangerous, though there are possible cases of evenomization in France attributed to this species (Emerit & Bonaric 1995).

Zoropsidae contains two genera: *Takeoa* Lehtinen 1967 and *Zoropsis* Simon 1878 (Platnick 1993). The family was previously known from the Palearctic region with records from the Canary Is-

lands on the west, and east through the circum-Mediterranean region and the Balkans to China, Japan and Korea (Roewer 1954:1284; Brignoli 1983: 591; Platnick 1989:504, 1993:587; 1997:611). *Zoropsis spinimana* has been reported from the circum-Mediterranean (Wunderlich 1994).

Zoropsis has been represented in two recent phylogenetic studies. In a study of the Lycosoidea and their kin, Griswold (1993) confirmed the monophyly of a Zoropsidae including *Zoropsis* and *Takeoa*. In that study, zoropsid synapomorphies were a membranous process on the papal tegulum (in addition to the conductor and median apophysis) (Fig. 2) and shallowly notched trochanters. Griswold et al. (1999) found that *Zoropsis, Acanthoctenus* and *Psechrus* exemplify a monophyletic Lycosoidea (in part) defined by the synapomorphic presence of claw tufts, grate-shaped tapetum in the indirect eyes (with homoplasy in Stiphidiidae), and the presence of a minor ampullate gland spigot nubbin on the posterior median spinnerets.

Zoropsis spinimana is easily recognized. It keys to Tengellidae in Roth's (1993) *Spider Genera of North America*; p. 37: couplet 5, Section III (eight-eyed spiders), Group I (cribellates). It differs from spiders placed in Roth's 'Tengellidae' (in his paper represented only by *Zorocrates*, which is now placed in Zorocratidae) by having the body patterned (Fig. 1) rather than unicolorous, having the posterior eye row strongly recurved (Fig. 1) rather than straight to weakly procurved, having 6–7 pairs of spines beneath tibia I (Fig. 1) rather than 4–5
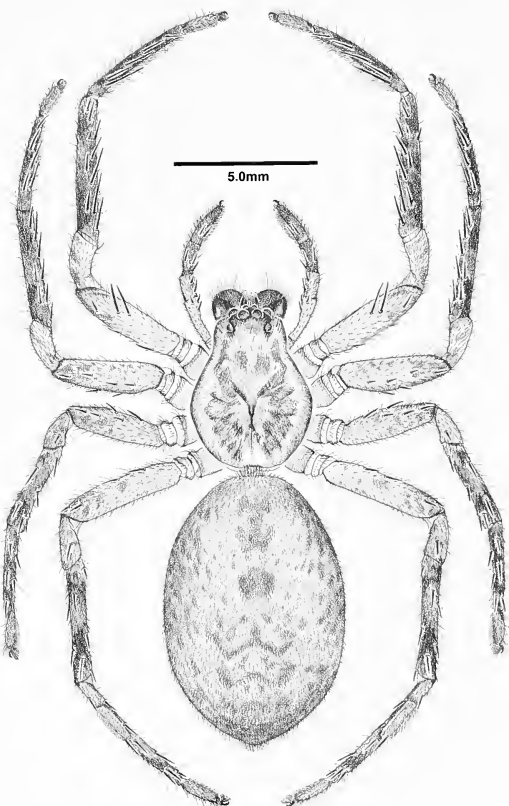
Figure 1.—Dorsal view of female *Zoropsis spinimana* (Dufour) from Sunnyvale, California.

pairs, and lacking the inferior tarsal claw from all tarsi (Griswold 1993, fig. 6) rather than retaining the inferior claw on tarsus I. Like other cribellate members of the Lycosoidea and their kin, *Zoropsis* has an oval calamistrum on metatarsus IV of females and juveniles (Fig. 1; Griswold 1993, fig. 1). The male palpus has a short, blunt embolus, hyaline conductor, hooked median apophysis and an additional, membranous process that cradles the embolus (Figs. 2, 5). The epigynum (Fig. 3) is unusual in having a central, digitiform scape, which is hollow (Fig. 4) and reminiscent of some araneids and some species of the South African lycosoid genus *Phanotea* Simon 1896 (Griswold 1994, figs. 79, 80).

This discovery adds another spider family to the list for the USA. Roth (1993) lists only 59 spider families occurring in the USA, but he maintains broad limits for several families now subdivided (Platnick 1993) including Agelenidae (which also includes Cybaeidae), Clubionidae (also including Corinnidae, Liocranidae, and Miturgidae), Linyphiidae (also includes Pimoidae), and Amaurobiidae (also includes Titanoecidae). Additionally, *Metaltella* is now placed in the Amphinectidae (Davies 1998; Griswold et al. 1999), *Zorocrates* in the Zorocratidae (Griswold et al. 1999), and *Liocranoides* and relatives in the Tengellidae (Platnick 1999). The addition of Zoropsidae increases the known spider fauna of the USA to 68 families.

Marge Moody of the California State Department of Agriculture (CDFA) sent the first specimens to
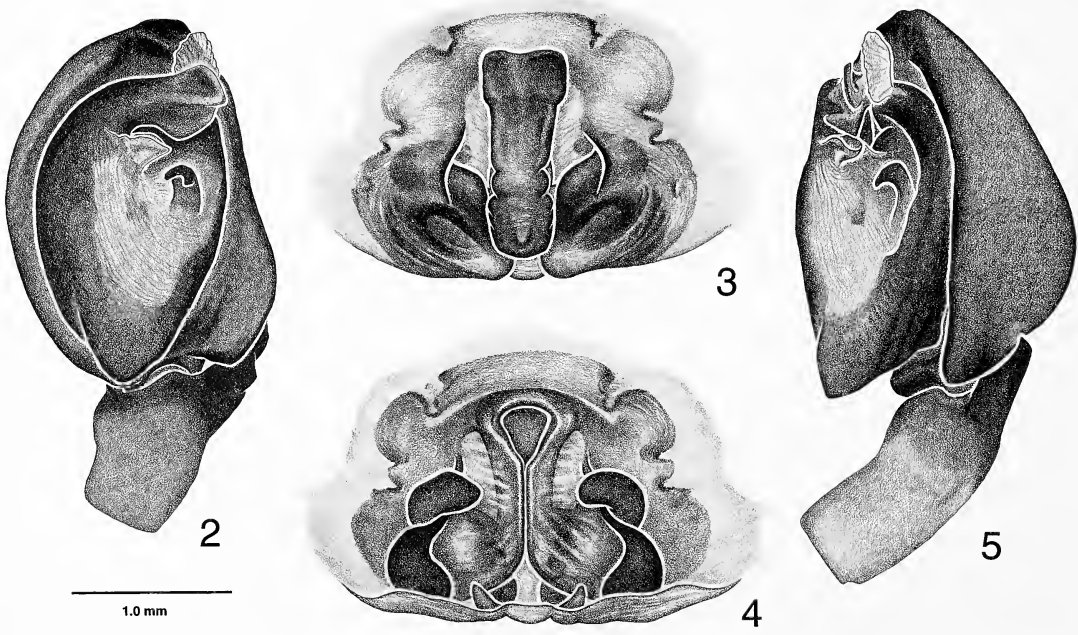
Figure 2–5.—Genitalia of *Zoropsis spinimana* (Dufour) from Sunnyvale, California. 2, Left male pedipalpus, ventral; 3, Epigynum, ventral; 4, Vulva, dorsal; 5, Left male pedipalpus, retrolateral.

us for determination. The habitus illustration and those of the male pedipalpus are by Michelle Schwengel. Her work was supported by the California Academy of Sciences through the Fellows' Artist Intern Program. The illustrations of the female epigynum and vulva are by Jenny Speckels, who was supported by the Exline-Frizzell Fund of the CAS Department of Entomology.

MATERIAL EXAMINED. CALIFORNIA: *Alameda County:* Oakland, SE side of Lake Merrit, in house, 24 September 1997, K. Lundstrom, 1♀, CAS. *Santa Clara County:* Cupertino, inside house, 21 October 1996, M. Beauregard, 1♂, CAS (CDFA #1174531). Sunnyvale, inside house, January–March 1999, V. Romano, 1♂1♀, CAS, (CDFA #993770). In house, 2 January 1998, J. Ward, 1♂, UCR; 3 February 1998, M. Murray, 1 penultimate ♂, CDFA (#1019167). Found in house, 12 February 1996, M. Beauregard, 1♂, CAS (CDFA #1019036). 27 April 1998, M. Nachand, 1♀, CDFA (#1174929). In house, 11 October 1995, M. Beauregard, 1♀, CAS (CDFA #1019033); 12 October 1995, M. Murray, 1♀, CAS (CDFA #1141353). In house, 22 October 1992, M. Beauregard, 1♀, CDFA (#750348). Santa Clara, 31 December 1997, M. Murray, 1♀, CDFA (#1019023). San Jose, in nursery, 1 April 1999, M. Murray, 1♀, CDFA (#1162149).

LITERATURE CITED

Brignoli, P.M. 1983. A catalogue of the Araneae described between 1940–1981. Manchester, 755 pp.

Davies, V.T. 1998. A revision of the Australian metaltellines (Araneae: Amaurobioidea: Amphinectidae: Metaltellinae). Invertebrate Taxonomy 12: 211–243.

Eberhard, W.G. & F. Pereira. 1993. Ultrastructure of cribellate silk of nine species in eight families and possible taxonomic implications (Araneae: Amaurobiidae, Deinopidae, Desidae, Dictynidae, Filistatidae, Hypochilidae, Stiphidiidae, Tengellidae). Journal of Arachnology 21:161–174.

Emerit, M. & J.C. Bonaric. 1995. Un cas d'envenimation de type loxoscélique attribué a l'araignée *Zoropsis spinimana* dans le midi de la France. Ann. soc. Hort. Hist. Nat. L'Hérault 135: 37–38.(spell out titles)

Griswold, C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). Smithsonian Contributions to Zoology 539:1–39.

Griswold, C.E. 1994. A revision and phylogenetic analysis of the African spider genus *Phanotea* Simon (Araneae: Lycosoidea). Ann., Sci. Zool., Mus. Roy. L'Afr. Centr., vol. 273:1–83.

Griswold, C., J. Coddington, N. Platnick & R. Forster. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). Journal of Arachnology 27:53–63.

Platnick, N.I. 1989. Advances in Spider Taxonomy: A Supplement to Brignoli's A Catalogue of the Araneae Described Between 1940 and 1981. Manchester, 673 pp.

Platnick, N.I. 1993. Advances in Spider Taxonomy, 1988–1991: with Synonymies and Transfers 1940–1980. New York Entomological Society, 846 pp.

Platnick, N.I. 1997. Advances in Spider Taxonomy, 1992–1995: With Redescriptions 1940–1980. New York Entomological Society, 846 pp.

Platnick, N.I. 1999. A Revision of the Appalachian spider genus *Liocranoides* (Araneae: Tengellidae). American Museum Novitates 3285:1–13.

Roewer, C.F. 1954. Katalog der Araneae von 1758 bis 1940, Vol. 2a:1–923. Bruxelles.

Roth, V.D. 1993. pider Genera of North America with Keys to Families and Genera and a Guide to Literature. American Arachnological Society, available from Dr. Jon Reiskind, Department of Zoology, University of Florida, Gainesville, Florida 32611 USA.

Wunderlich, J. 1994. Zur Kenntnis der West-Paläarktischen Arten der Gattung *Zoropsis* Simon 1878 (Arachnida: Araneae: Zoropsidae). Beitraege Aran., 4:723–727.

SHORT COMMUNICATION

DISPERSAL OF *STEGODYPHUS DUMICOLA* (ARANEAE, ERESIDAE): THEY DO BALLOON AFTER ALL!

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ABSTRACT.   There has been some controversy about whether adult females of social *Stegodyphus* disperse by ballooning. Here we show that adult *Stegodyphus dumicola* (Eresidae) Pocock 1898 are able to gain up-lift by releasing a very large number of threads. The threads fan out widely from the spider's body and form a triangular sheet. This previously unknown ballooning mechanism, enables even large spiders to disperse over large distances.

Keywords: Eresidae, *Stegodyphus*, dispersal, ballooning, social spider

Dispersal by ballooning appears to be restricted to very small spiders and is mainly a strategy of juvenile spiders that disperse shortly after their emergence from the eggsacs (Decae 1987; Foelix 1996). The probability of ballooning as a function of spider size quickly approaches zero when the body mass exceeds 1 mg. Suter (1999) stated that large spiders are unlikely to balloon because thermal and climatic conditions are rarely favorable. In addition, unpredictable patch quality and low survival probability of ballooning spiders should make this strategy unattractive for adult spiders.

Wickler & Seibt (1986), however, observed a single adult *Stegodyphus mimosarum* (Eresidae) Pavesi 1883 ballooning; and Crouch et al. (1998) reported that during a mass dispersal event, adults of *S. mimosarum* became airborne and were carried for several meters by strong, gusting winds. In the latter case, it is not clear if the spiders ballooned, i.e., if they lifted off the surface by means of silk, or if they were blown horizontally and used the silk to anchor themselves. *Stegodyphus mimosarum* is one of three social species of the

genus and is distributed throughout southern Africa. Social *Stegodyphus* Simon 1873 are characterized by dispersal of adult females that usually have a body mass larger than 100 mg. Wickler & Seibt (1986) described the single ballooning individual as flying with 3–4 silk strands that were no longer than 3–4 m in a barely perceptible breeze. Henschel et al. (1995) used these figures in Suter's (1991) formula and concluded that with the given length of silk and the described wind velocity, an adult spider of that size (80–150 mg) could not become airborne. The apparent contradiction can have two possible causes: either the observation was misinterpreted or the parameters used in the formula did not exactly describe the observed situation. Recent observations now enable us to clarify the issue.

Between 25–31 January 2000 we checked 31 colonies of *Stegodyphus dumicola* Pocock 1898 on a daily basis. (Voucher specimen are deposited at the National Museum in Windhoek, Namibia.) The nests were evenly distributed in an area of approximately 70,000 m² (7 ha). The study site was on the farm Omdraai, located 100 km southeast of Windhoek,

Namibia. The days were hot (28–33 °C), and there was almost no wind. On such days, rising thermals occur characteristically during the warm, calm hours of the day. On 27 January, around noon, 20 females of one colony were seen "tiptoeing" on the highest strand of the web. Tiptoeing behavior occurs as a prelude to ballooning: the spider stands on raised legs with the abdomen pointed upwards at an angle to the prosoma. In this position, silk released from the spinnerets will rise even in an almost imperceptible breeze (Foelix 1996). We observed these females releasing silk, and some became airborne. However, silk became snagged on nearby bushes so that the spiders landed between 1–8 m away from their nest of origin. During the late afternoon of the following day the same behavior was observed in three other nests. On one occasion, more than six spiders in quick succession were lifted almost straight up and could be observed gaining height for a few sec. We lost sight of the spiders after they reached a height of approximately 30 m. These spiders were the size of adult females, between 7–14 mm body length (see Kraus & Kraus 1988).

Perhaps the most important aspect of our observation is that the spiders used a very large number of silk strands to become airborne. At least tens to hundreds of threads were seen silhouetted against the sky. The threads fanned out widely from the spider's body and formed a triangular sheet with a length and width of about 1 m at its distal end. The silk that was released was not combed, appeared to be produced quickly, and did not tangle or clump once released.

In the 31 nests observed, females in 10 colonies were observed tiptoeing as spiders prepared to release silk threads. In two colonies we saw bridging, a common method of dispersal in *Stegodyphus* (Henschel et al. 1995); and in one colony we saw ballooning. We measured the sizes of all nests by using the two largest diagonals. Ten nests that produced dispersers were significantly larger ($n = 10$; mean $\pm$ SE $= 155.2 \pm 20.23$ mm^2) than nests without dispersers ($n = 21$; mean $\pm$ SE $= 60.5 \pm 9.26$ mm^2; Kruskal-Wallis test: Z $= 3.61$, $P < 0.0003$). As nest size is related to colony size (Henschel 1998), this indicates that only larger colonies produced dispersing females.

In order to assess the reproductive status of dispersing individuals, nine females were collected while tiptoeing, which is indicative of imminent dispersal, and were kept in the laboratory without access to males. Seven of these females produced eggsacs within 6 wk after collection. This indicates that most, if not all dispersers are potentially capable of founding new colonies after establishing a new nest at their destination.

We did not observe males dispersing. Interestingly, 10 out of 17 collected colonies showed an unusual sex ratio of 25–52% males. *Stegodyphus* colonies usually have female-biased sex ratios (14–21.2% males) and the sex-ratio bias is primary (Avilés et al. 1999). Thus, the most likely explanation for the reduction in bias is that the majority of the females had left the colony whereas the males did not disperse.

Ballooning on multiple strands is a dispersal mechanism in spiders that has never been described before. By using multiple strands even large adult spiders may be able to disperse over great distances and to colonize new habitats. This has to be taken into consideration in the future when investigating population genetics and structure in the social *Stegodyphus*.

There are a number of questions that remain open. Which glands produce the ballooning silk? The large number of threads would suggest that cribellate silk might be used; but if so, it is apparently not combed out. What keeps the multiple threads from collapsing or coalescing? Perhaps electrostatic forces play a role in keeping the threads apart. Is the lift generated by such a large number of threads equal to the sum of the forces acting on each one, or do the threads indeed form a sheet dense enough to be considered as a whole? Finally, is ballooning the regular dispersal mode used by social *Stegodyphus*? Colonies appear to send out dispersers only in one particular state of development, namely after the majority of females have matured and mated and before egg-laying begins (Henschel et al. 1995; Henschel 1998). Thus, for dispersal by ballooning, weather conditions must be suitable during a rather narrow time window. Long-term monitoring of dispersal and climate will be required to answer this question.

LITERATURE CITED

Avilés, L., C. Varas & E. Dyreson. 1999. Does the African social spider *Stegodyphus dumicola* control the sex of individual offspring? Behavioural Ecology and Sociobiology 40:237–245.

Decae, A.E. 1987. Dispersal: Ballooning and other mechanisms. Pp. 348–358. In Ecophysiology of Spiders. (W. Nentwig, ed.). Springer Verlag, Heidelberg.

Foelix, R.F. 1996. Biology of Spiders, 2nd ed. Oxford Univ. Press and Georg Thieme Verlag, New York.

Henschel, J.R. 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). Journal of Arachnology 26:61–69.

Henschel, J.R., J. Schneider & Y. Lubin. 1995. Dispersal mechanisms by the spiders *Stegodyphus*: Do they balloon? Journal of Arachnology 23:202–204.

Humphrey, J.A.C. 1987. Fluid mechanical constraints on spider ballooning. Oecologia 73:469–477.

Kraus O. & M. Kraus. 1988. The genus *Stegodyphus* (Arachnida, Araneae). Sibling species. Species groups, and parallel origin of social living. Verhandlungen des naturwissenschaftlichen Vereins Hamburg 30:151–254.

Suter, R.B. 1991. Ballooning in spiders: Results of wind tunnel experiments. Ethology, Ecology & Evolution 3:13–25.

Suter, R.B. 1999. An aerial lottery: The physics of ballooning in a chaotic athmosphere. Journal of Arachnology 27:281–293.

Wickler, W. & U. Seibt. 1986. Aerial dispersal by ballooning in adult *Stegodyphus mimosarum*. Naturwissenschaften 73:628–629.

SHORT COMMUNICATION

A TECHNIQUE FOR INDIVIDUALLY IDENTIFYING TARANTULAS USING PASSIVE INTEGRATED TRANSPONDERS

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ABSTRACT. A surgical technique for implanting passive integrated transponders into theraphosid spiders is described. An effecitve procedure for anesthesia was developed. Transponders were implanted in the opisthosomas of 12 spiders. No mortality occurred, and all spiders regained normal behavior. In simulated burrows, tarantulas could be identified to a depth of 16 cm.

Keywords: PIT tags, spider marker, Theraphosidae

No complete life history study of a theraphosid spider has appeared since the pioneering work of Baerg (1958). A necessary component of such endeavors is the application of a marker that enables the researcher to permanently distinguish individual spiders. Marking theraphosids is particularly difficult because they molt regularly (Baerg & Peck 1970) throughout their long life of 20 years or more in some females (Marshall 1996). A marker should be internal and identifiable for many years to be useful in long-term life history studies of tarantulas.

Widespread use of passive integrated transponders, which are commonly known as PIT tags, in vertebrate studies suggests that an application might be found for tarantulas. These devices are small and can be read by a hand-held reader emitting low-frequency radio waves. The transponder signal is received, decoded, and displayed by the reader as a unique 10-character code. The transponders are hermetically sealed in biocompatible glass and appear to have an unlimited life span. Although widely used by zoo personnel, vertebrate field biologists and veterinarians (Elbin & Burger 1994), this is the first time—to our knowledge—that PIT tags have been used in an invertebrate. For large arachnids this technology provides the perfect marker, being permanent, unrecognizable and untransferable to other spiders, benign in its effect on survival, and easy to apply especially under field conditions (Evans & Gleeson 1998).

The technique was tested on adults of *Aphonopelma baergi* (*n* = 4; body length 38–47 mm), *Brachypelma albopilosum* (*n* = 4; body length 38–75 mm), and *Grammostola pulchra* (*n* = 4; body length 62–68 mm). *Aphonopelma* were collected as adults, 10 km north of Jessieville, Garland County,

Arkansas. *Brachypelma* and *Grammostola* were obtained as captive-bred juveniles from commercial suppliers in the United States and reared to adulthood. Transponder implantations were performed in the veterinary hospital at the Memphis Zoo and field trials were conducted on zoo grounds. We used the Trovan® (Grossbuilesheimer, Str. 56, Euskirchen 16, Germany) reader (Model LID 500) and transponders in all trials. The location for implantation of the transponder was on the dorsolateral aspect of the opisthosoma in an area between the heart and the intestinal tract (Fig. 1). Tarantulas were restrained by hand during the procedure. A 20-gauge hypodermic needle was used to scrape the setae from a 1.5 × 1.5 mm area of the opisthosoma, and swabbed with a 10% povidone-iodine solution. The sterile needle was used to cut the exoskeleton. The sharp apical edge of the needle was used like a scalpel rather than creating a puncture wound. The transponder was inserted into the opisthoma with sterile mosquito forceps. The surgical site was then swabbed dry and several drops of n-butyl cyanoacrylate adhesive glue (Vetabond®, 3M Animal Care Products, St. Paul, Minnesota) were used to close the wound. The entire procedure took 2–3 minutes per spider. Leakage of haemolymph varied. In one instance there was a moderate loss of fluid from the site, but the spider recovered fully.

Four of the spiders (*A. baergi, n* = 2; *B. albopilosum, n* = 2) were anesthetized prior to implantation. Spiders were immobilized with isoflurane (Iso-thesia℗, Abbott Laboratories, North Chicago, Illinois). A cottonball was soaked in the anesthetic agent and placed in a small plastic container away from the spider. The effect of the anesthetic was monitored by leg movement. As the spiders became
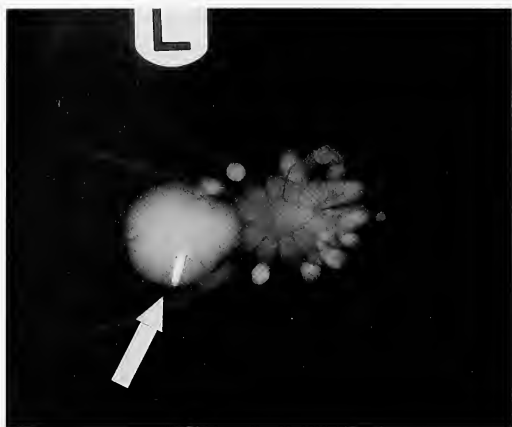
Figure 1.—Radiograph showing passive integrated transponder (arrow) implanted in a *Grammostola pulchra*.

anesthetized the legs contracted followed by relaxation.

Spiders which were not anesthetized during transponder implants accepted food within several hours, suggesting they had not been severely traumatized by the procedure. Anesthetized spiders required 2–3 hours post-surgical recovery time before normal movement was exhibited. All spiders which had implants completed ecdysis within 3–7 months. After molting, no evidence of the implants was noted. All spiders were preserved after two years. Voucher specimens were deposited in the Field Museum of Natural History, Chicago.

To assess the limits of the reader in decoding the transponder signal from implanted spiders *in situ*, we conducted trials using artificial burrows. A natural burrow replica was prepared by boring a 5 cm diameter hole at an 80° angle to a depth of 20 cm. Trials were conducted in hard-packed humus on a rainy day to simulate typical field conditions for many species of theraphosids. Spiders were identifiable in the burrows at a depth of up to 16 cm. This distance approaches the 18–20 cm detection limit of the reader across unobstructed space.

This technique is best suited for long term field studies of large, long-lived arthropods such as theraphosid spiders, scolopendrid centipedes, and scorpions. The sensitivity-level of the reader precludes identification of theraphosids resting at the bottom of deep burrows. However, tarantulas could easily be identified at night while they are passively foraging at their burrow entrance, eliminating the time-consuming process of capture and handling. Anesthesia prior to implantation is unnecessary and not convenient under field conditions, but it is tolerated by the spiders. Untrained personnel may consider anesthetizing specimens until they become more adept at inserting the transponders.

Short-term movements such as the migration of male tarantulas during the breeding season can be monitored by radio telemetry (Janowski-Bell & Horner 1999). However, limitations in battery life, durability of transmitter adhesion, and the potential for these transmitters to interfere with normal behavior make radio telemetry unsuitable for studies conducted over a longer time scale. We believe this new application for PIT tags offers a way to study previously inaccessible aspects of theraphosid spider biology such as growth, survivorship, and the movements of individuals over their entire lives.

LITERATURE CITED

Baerg, W.J. 1958. The Tarantula. Univ. Kansas Press. Lawrence, Kansas. 88 pp.

Baerg, W.J. & W.B. Peck. 1970. A note on longevity and molt cycle of two tropical theraphosids. Bulletin of the British Arachnological Society 1:107–108.

Elbin, S.B. & J. Burger. 1994. Implantable microchips for individual identification in wild and captive populations. Wildlife Society Bulletin 22:677–683.

Evans, T.A. & P.V. Gleeson. 1998. A new method of marking spiders. Journal of Arachnology 26: 382–384.

Janowski-Bell, M.E. & N.V. Horner. 1999. Movement of the male brown tarantula, *Aphonopelma hentzi* (Araneae, Theraphosidae) using radio telemetry. Journal of Arachnology 27:503–512.

Marshall, S.D. 1996. Tarantulas and Other Arachnids. Barron's Educ. Ser., Inc., Hauppauge, New York. 104 pp.

SHORT COMMUNICATION

SPIDERS FEEDING ON EARTHWORMS

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ABSTRACT. A house spider (*Tegenaria atrica* C.L. Koch 1843, Agelenidae) was observed, filmed and photographed while feeding on an earthworm. An extensive search in the literature revealed that several arachnologists had noted spiders feeding on earthworms, altogether in 11 different families. Earthworm-eating spiders belong mostly to larger sized species dwelling near the ground in woodlands and grasslands. Since earthworms have a high protein content, they could be a welcome supplement to the spider's usual insect diet.

Keywords: Spiders, prey, foraging, diet, earthworm

Most spiders are polyphagous predators that prey predominantly on insects and to a lesser extent on other spiders (Riechert & Harp 1987; Nentwig 1987; Nyffeler et al. 1994). Spiders feeding on non-arthropod prey have rarely been reported (see Foelix 1996). That earthworms may be included in a spider's diet has not been recognized so far. However, this is exactly what was noted by one of us (H.M.) in September 1999 in Herznach, Switzerland: a *Tegenaria atrica* C.L. Koch 1843 (Agelenidae) was observed, filmed and photographed while feeding on an earthworm of 14 cm length (Figs. 1, 2). Bristowe's book *"The Comity of Spiders"* (1941), which includes a long chapter on 'The Food of Spiders,' revealed nothing on this peculiar type of feeding. Likewise, books on the biology of earthworms make no reference to spiders as enemies (see Edwards & Lofty 1972; MacDonald 1983; Lee 1985). Thus, the question arises whether our observation on *Tegenaria* was an isolated case or whether similar incidences have been noticed elsewhere.

An extensive literature search was conducted in order to find any information available on spiders feeding on earthworms. The search was based largely on the "Liste des Travaux Arachnologiques" (1968–1999), published by the International Society of Arachnology (for-

merly the C.I.D.A., Paris, France). In addition, an international arachnology discussion group was contacted via Internet. Altogether about 30 reports on spiders consuming earthworms were gathered (Table 1). Spiders from 11 different families are known to feed on earthworms. In two instances an unidentified species of *Tegenaria* (possibly *agrestis* (Walckenaer 1802)) was found by Yann Evenou (pers. commun.) preying on earthworms in the field, thus confirming our observation on *Tegenaria*. Furthermore, Günter Schmidt (pers. commun.) fed *Tegenaria ferruginea* (Panzer 1804) in captivity with earthworms of 8–10 cm length.

One of the earliest published reports on spiders consuming earthworms is that of Gerhardt & Kaestner (1937). Spiders from the mygalomorph genus *Atypus* Latreille 1804 (Atypidae), which inhabit silk tubes in the ground, were observed pulling earthworms into the tube and eating them. However, Bristowe (1958) expressed some reservations: "... Some early naturalists thought *Atypus* must emerge at night to hunt prey, whilst others were convinced that she subsisted on earthworms ..." and further "the idea that *Atypus* feeds largely on earthworms gains no support from examination or tests." Nevertheless, he admitted: "... experiment with

Figures 1, 2.—Spider feeding on an earthworm. 1. *Tegenaria atrica* trying to pull up its victim, an earthworm, onto its sheet web; 2. Dorsal close-up view of *Tegenaria* feeding on the front end of an earthworm.

worms placed on the surface 'finger' has shown that they get torn in the encounter, leaving at most a part of their bodies in the spider's possession which cannot readily be hauled into the tube. Although *Atypus* may suck the worm's juices for a time, she does not appear to finish the meal." Crome (1967) successfully fed *Atypus affinis* Eichwald 1830 in captivity with earthworms.

Hadronyche versuta (Rainbow 1914) (Hexathelidae), a mygalomorph spider from Australia that dwells in a silk tube burrow in the ground, also includes earthworms in its diet (Brunet 1998). Still another case of a mygalomorph spider feeding on earthworm prey was observed by Ricardo Ott (pers. commun.) in the rainforest of the Amazon: a large *Theraphosa blondi* (Latreille 1804) (Theraphosidae) was feeding on an earthworm of 30 cm length. Theraphosidae, representing 12 different species and 8 genera, have been seen preying on earthworms in captivity (Yann Evenou

& Jakob Walter pers. commun.). According to Brunet (1998), insects and earthworms form the staple diet of the mygalomorphs. Large earthworms (up to 20 cm) were also fed in captivity to the fishing spider *Dolomedes fimbriatus* (Clerck 1757) (Pisauridae) (Schmidt 1957).

Feeding on earthworms is probably a rarity among spiders (Wolfgang Nentwig pers. commun.). Spiders that spin a catching web in the higher strata of the vegetation, with which they capture small winged insects from the aerial plankton, will rarely, if ever, get in contact with earthworms. Although the orb web spider *Araneus diadematus* Clerck 1757 accepted earthworms in captivity (Nyffeler unpubl. data; Table 1), it is not expected to show this behavior in the field. During hundreds of hours of field observations, spiders feeding on earthworms were seen very rarely (Nyffeler 1982) or not at all (Zimmermann & Spence 1989). Feeding on earthworms seems to occur

Table 1.—Spiders feeding on earthworms (published and unpublished observations).

Species	Family	Typical adult body length (♀)	Typical habitat
Araneomorphae:			
Tegenaria atrica C. L. Koch 1843	Agelenidae	15 mm	Woodland and gardens, under stones
Tegenaria sp. Latreille 1804	Agelenidae	15 mm	Grassland, ground
Tegenaria ferruginea (Panzer 1804)	Agelenidae	14 mm	Woodland, crevices in tree trunks
Amaurobius ferox (Walckenaer 1830)	Amaurobiidae	15 mm	Woodland, under stones and logs
Amaurobius fenestralis (Stroem 1768)	Amaurobiidae	8 mm	Woodland, under stones and logs
Segestria florentina (Rossi 1790)	Segestriidae	20 mm	Under stones and logs
Araneus diadematus Clerck 1757	Araneidae	15 mm	Woodland, grassland, bushes
Xysticus sp. C. L. Koch 1835	Thomisidae	7 mm	Grassland, low vegetation or ground
Xysticus sp. C L. Koch 1835	Thomisidae	7 mm	Grassland, low vegetation or ground
Pardosa sp. C. L. Koch 1847	Lycosidae	6 mm	Marshland, low vegetation or ground
Trochosa terricola Thorell 1856	Lycosidae	14 mm	Woodland, grassland, under stones
Dolomedes fimbriatus (Clerck 1757)	Pisauridae	20 mm	Swampy areas, low vegetation
Ancylometes rufus (Walckenaer 1837)	Pisauridae	35 mm	Tropical rainforest, ground
Ctenus amphora Mello-Leitao 1930			
Ctenus crulsi Mello-Leitaeo 1930	Ctenidae	17 mm	Tropical rainforest, ground
Mygalomorphae:			
Atypus affinis Eichwald 1830	Atypidae	15 mm	Woodland slopes, ground
Atypus sp. Latreille 1804	Atypidae	15 mm	Slopes with low vegetation, ground
Atypus affinis Eichwald 1830	Atypidae	15 mm	Woodland slopes, ground
Atypus affinis Eichwald 1830	Atypidae	15 mm	Woodland slopes, ground
Hadronyche sp. L. Koch 1873	Hexathelidae	30 mm	Subtropical rainforest, ground
Hadronyche versuta (Rainbow 1914)	Hexathelidae	30 mm	Subtropical rainforest, ground
Theraphosa blondi (Latreille 1804)	Theraphosidae	100 mm	Tropical rainforest, ground burrow
Theraphosa blondi (Latreille 1804)	Theraphosidae	100 mm	Tropical rainforest, ground burrow
Aphonopelma anax (Chamberlin 1940)	Theraphosidae	60 mm	Grassland, scrubland, ground burrow
Aphonopelma pallidum (F.O.P.-Cambridge 1897)	Theraphosidae	40 mm	Subtropical scrubland, ground burrow
Brachypelma albopilosum Valerio 1980	Theraphosidae	70 mm	Tropical rainforest, ground burrow
Brachypelma smithi (F.O.P.-Cambridge 1897)	Theraphosidae	70 mm	Woodland, grassland, ground burrow
Brachypelma vagans (Ausserer 1875)	Theraphosidae	60 mm	Subtropical forest, ground burrow
Chromatopelma cyaneopubescens (Strand 1907)	Theraphosidae	50 mm	Subtropical scrubland, ground
Grammostola iheringi (Keyserling 1891)	Theraphosidae	100 mm	Tropical rainforest, ground burrow
Grammostola pulchra Mello-Leitao 1921	Theraphosidae	60 mm	Grassland, ground
Hysterocrates ederi Charpentier 1995	Theraphosidae	70 mm	Tropical rainforest, ground burrow
Lasiodora parahybana Mello-Leitao 1917	Theraphosidae	70 mm	Rainforest, ground
Poecilotheria regalis Pocock 1899	Theraphosidae	60 mm	Monsoon forest, hollow trees

Table 1.—Extended.

Web type	Location of observation	Source
Sheet (ecribellate)	Field	This paper
Sheet (ecribellate)	Field	Yann Evenou (unpubl.)
Sheet (ecribellate)	Captivity	Günter Schmidt (unpubl.)
Sheet (cribellate)	Captivity	Günter Schmidt (unpubl.)
Sheet (cribellate)	Captivity	Günter Schmidt (unpubl.)
Snare (ecribellate)	Field	Yann Evenou (unpubl.)
Orb (ecribellate)	Captivity	Martin Nyffeler (unpubl.)
None	Field	Nyffeler (1982)
None	Field	Jakob Walter (unpubl.)
None	Field	Vogel (1971)
None	Field	Yann Evenou (unpubl.)
None	Captivity	Schmidt (1957)
None	Field	Ricardo Ott & Clarissa Azevedo (unpubl.)
None	Field	Hubert Hoefer (unpubl.)
Silk tube burrow	Field	Savory (1926)
Silk tube burrow	Field?	Gerhardt & Kästner (1937)
Silk tube burrow	Captivity	Bristowe (1958)
Silk tube burrow	Captivity	Crome (1967)
Silk tube burrow	Captivity	David Rowell (unpubl.)
Silk tube burrow	Field	Brunet (1998)
None	Field	Ricardo Ott (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Jakob Walter (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)
None	Captivity	Yann Evenou (unpubl.)

among spiders that dwell on the ground—under stones and logs, in the leaf litter and moss-covered patches, in cracks in the soil, and in earth burrows and silk tube burrows—or on low vegetation near the ground in woodlands and grasslands (i.e., habitats where earthworms are abundant) (Table 1). Web-building and nonweb-building spiders alike have been observed eating earthworms. They belong predominantly to larger species (> 10 mm body length, see Table 1), though there are exceptions. For instance, Nyffeler (1982) found a crab spider of the genus *Xysticus* C.L. Koch 1835, about 7 mm in length, sucking an earthworm of approximately 2 cm in length. *Xysticus* spp., nonweb-building spiders equipped with powerful front legs and supposedly potent venom, are able to subdue prey 2–3 times their own size (see Gertsch 1979; Nentwig & Wissel 1986). Among web-building spiders reported feeding on earthworms (Table 1), species that make sheet webs (i.e., *Tegenaria* and *Amaurobius*) or use a silk tube (i.e., *Atypus* and *Hadronyche*) dominate. Such webs function as effective traps for the capture of crawling prey organisms. Surprisingly, some nocturnal ground-surface dwellers (e.g., Gnaphosidae and Dysderidae)—expected often to encounter earthworms—are missing in the table.

In terrestrial ecosystems, most of the net primary production is used by detritivores and decomposers in the soil, resulting in a huge earthworm biomass which serves a variety of predators as food (see MacDonald 1983; Halaj & Cady 2000). Earthworm tissue has a high protein content ($\approx$60–70%, dry weight) (MacDonald 1983; Lee 1985); thus an earthworm should be a welcome meal to a spider. Table 1 includes, among others, species from the families Pisauridae, Hexathelidae and Theraphosidae, which exhibit opportunistic feeding (broad diets) (e.g., Zimmermann & Spence 1989; Brunet 1998; Yann Evenou pers. commun.). It is not surprising that the diets of these nonspecific feeders also include earthworms. Such species are adapted to a broad range of prey types that optimizes their survival during periods of food shortage. Predation on earthworms may be of ecological significance for some larger spiders (e.g., mygalomorphs) by supplementing their insect diets (see Brunet 1998).

LITERATURE CITED

Bristowe, W.S. 1941. The Comity of Spiders. Vol. II. Ray Society, London.

Bristowe, W.S. 1958. The World of Spiders. Collins, London.

Brunet, B. 1998. Spiderwatch: A Guide to Australian Spiders. New Holland Publishers, Sydney.

Crome, W. 1967. Wirbellose Tiere. Rowohlt Taschenbuch Verlag, Hamburg.

Edwards, C.A. & J.R. Lofty. 1972. Biology of Earthworms. Chapman & Hall, London.

Foelix, R.F. 1996. Biology of Spiders (2nd ed.). Oxford Univ. Press and Thieme Verlag, New York.

Gerhardt, U. & A. Kaestner. 1937. 8. Ordnung der Arachnida: Araneae = Echte Spinnen = Webspinnen. *In* Handbuch der Zoologie (W. Kükenthal & T. Krumbach, eds.). de Gruyter, Berlin.

Gertsch, W.J. 1979. American Spiders (2nd ed.). Van Nostrand, New York.

Halaj, J. & A.B. Cady. 2000. Diet composition and significance of earthworms as food of harvestmen (Arachnida: Opiliones). American Midland Naturalist 143:487–491.

Lee, K.E. 1985. Earthworms, Their Ecology And Relationships With Soils And Land Use. Academic Press, London.

MacDonald, D.W. 1983. Predation on earthworms by terrestrial vertebrates. Pp. 393–414. *In* Earthworm Ecology. (J.E. Satchell, ed.). Chapman and Hall, London, New York.

Nentwig, W. 1987. The prey of spiders. Pp. 249–263. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin, New York.

Nentwig, W. & C. Wissel. 1986. A comparison of prey lengths among spiders. Oecologia 68:595–600.

Nyffeler, M. 1982. Field Studies on the Ecological Role of the Spiders as Insect Predators in Agroecosystems. Ph.D. dissertation. Swiss Federal Institute of Technology, Zurich.

Nyffeler, M., W.L. Sterling & D.A. Dean. 1994. How spiders make a living. Environmental Entomology 23:1357–1367.

Riechert, S.E. & J.M. Harp. 1987. Nutritional ecol-
    ogy of spiders. Pp. 645–672. *In* Nutritional Ecol-
    ogy of Insects, Mites, and Spiders. (F. Slansky &
    J.G. Rodriguez, eds.). John Wiley, New York.
Savory, T.H. 1926. British Spiders (Their Haunts
    And Habits). Clarendon Press, Oxford.
Schmidt, G. 1957. Einige Notizen über *Dolomedes
    fimbriatus* (Cl.). Zoologischer Anzeiger 158:83–
    97.

Vogel, B.R. 1971. Individual interactions of *Par-
    dosa.* Armadillo Papers 5:1–12.
Zimmermann, M. & J.R. Spence. 1989. Prey use
    of the fishing spider *Dolomedes triton* (Pisauri-
    dae, Araneae): An important predator of the
    neuston community. Oecologia 80:187–194.

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Title page.—The title page will include the complete name, address, and telephone number of the author with whom proofs and correspondence should be exchanged, a FAX number and electronic mail address if available, the title in capital letters, each author's name and address, and the running head (see below).

Abstract.—The heading in capital letters should be placed at the beginning of the first paragraph set off by a period. A second abstract, in a language pertinent to the nationality of the author(s) or geographic region(s) emphasized, may be included.

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Text.—Double-space text, tables, legends, etc. throughout. Three categories of headings are used. The first category (METHODS, RESULTS, etc.) is typed in capitals and on a separate line. The second category of heading, in bold type, begins a paragraph with an indent and is separated from the text by a period and a dash. The third category of heading may or may not begin a paragraph but is italicized and separated from the text by a colon. Use only the metric system unless quoting text or referencing collection data. All decimal fractions are indicated by the period (e.g.,-0.123).

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Lombardi, S.J. & D.L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (dragline) of *Nephila clavipes* (Araneae, Tetragnathidae). Journal of Arachnology 18:297-306.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Running head.—The author's surname(s) and an abbreviated title should be typed all in capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style, or contact the Subject Editor for Systematics. Papers containing the original taxonomic description of the focal arachnid taxon should be listed in the Literature Cited section.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (usually three) should be included. Tables may not have footnotes; instead, include all information in the legend. Make notations in the text margins to indicate the preferred location of tables in the printed text.

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Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1–4.—*A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us* holotype male; 33, 34. *A-us y-us* male. Scale = 1.0 mm.

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CONTENTS

The Journal of Arachnology

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Cover photo: Scorpion (*Centruroides* sp.) with young. Photo taken by the late M.W. Tyler of Umatilla, Florida about 1953.

Publication date: 31 August 2001

♾ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

AUTOECOLOGY AND DESCRIPTION OF *MUMMUCIA MAURYI* (SOLIFUGAE, MUMMUCIIDAE), A NEW SOLIFUGE FROM BRAZILIAN SEMI-ARID CAATINGA

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ABSTRACT.   The Brazilian solifuge *Mummucia mauryi* new species (Solifugae, Mummuciidae) from sand dunes of the São Francisco River, in semiarid caatinga domain, is herein described, with illustrations of the main taxonomic characters. This is the first species of Solifugae described from the Brazilian caatinga. The specimens were collected in pitfall traps during both the rainy and dry seasons. It exhibits diurnal activity and a clumped distribution (Morisita's index = 3.32 and 1.38 for rainy and dry season, respectively). Sun-exposed areas were avoided during the dry season, when preference for the cactacean *Opuntia inamoena* was detected. We suggest this association is related to predator avoidance.

RESUMO.   O solífugo *Mummucia mauryi* (Solifugae, Mummuciidae) é descrito a partir de exemplares coletados nas dunas interiores do Rio São Francisco (BA), com ilustrações dos principais caracteres taxonômicos. Esta é a primeira espécie de Solifugae descrita para o domínio da caatinga semi-árida. Estudos sobre a autoecologia indicam atividade diurna; distribuição do tipo agregado (índice de Morisita = 3.32 e 1.38 para as estações chuvosa e seca, respectivamente); preferência negativa por áreas mais expostas à insolação durante a estação seca e preferência pela cactácea *Opuntia inamoena*, o que sugerimos estar relacionado à proteção contra predadores.

Keywords: Arachnida, microhabitat, Solpugida, systematics

Knowledge of the order Solifugae in the Neotropical Region is very limited, especially for the portion of South America occupied by Brazil, which includes distinctive environments such as caatinga and cerrado. In this area, studies on Solifugae are scarce and there are a few distributional records, some of which were unfortunately excluded from some world maps (Savory 1964; Punzo 1998). Maury (1984) comprehensively listed and annotated all Brazilian records: *Gaucha fasciata* Mello-Leitão 1924 (Mummuciidae) from Porto Alegre, State of Rio Grande do Sul (Mello-Leitão, 1924); *Metacleobis fulvipes* Roewer 1934 (Mummuciidae) from Cuiabá, State of Mato Grosso (Roewer 1934); *Ammotrecha friedlaenderi* Roewer 1954 (Ammotrechidae) from Mendes, State of Rio de Janeiro (Roewer 1954); an undetermined species of Ammotrechidae, from State of Roraima, Brazil (Maury 1982); and, at a later date, an undetermined

species of Ammotrechidae from Manaus, State of Amazonas (Höfer & Beck 1995).

Unfortunately, these records are mere occurrence registers; and except for the record mentioned by Höfer & Beck (1995), there is no ecological information about the species. Moreover, *Ammotrecha friedlaenderi* and *Metacleobis fulvipes* are known only from their types and the records from Roraima and Manaus are immature individuals and therefore cannot be identified at this time.

Recently, new records of Solifugae in Brazilian Amazonia and cerrado have been noted (Rocha & Cancello 1997), extending the known distribution and habitats in South America, which is probably greater than present records indicate. In addition to our poor understanding of the systematics and diversity of Neotropical Solifugae, very little is known about their ecology and behavior. Most of the ecological studies on these arachnids deal
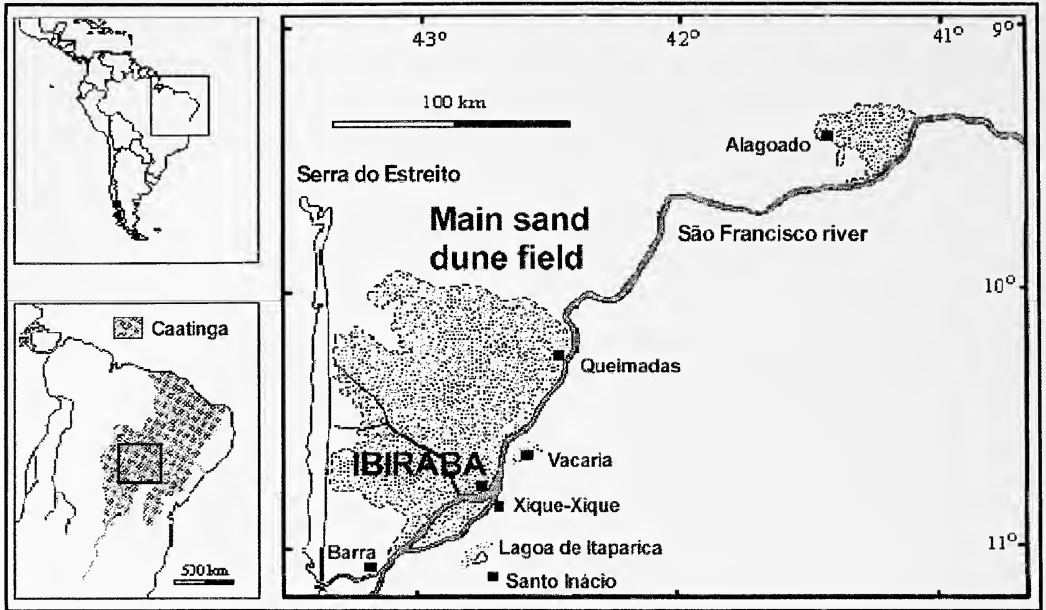
Figure 1.—Continental sand dunes of São Francisco river, Brazil, in the caatinga morphoclimatic domain showing the studied area at Ibiraba.

with North American and African species. This is the first study presenting data on the ecology of a Brazilian solifuge. In the present paper *Mummucia mauryi* new species is described from the State of Bahia, in the Brazilian semi-arid caatinga domain. Ecological data, including circadian activity, spatial distribution pattern and microhabitat preferences are discussed.

METHODS

Terminology used in the description such as "bristles," "setae" and "spines" are used according to Muma (1951). Some of these structures, bearing a bifurcation at the tips, are called "bifid bristles," etc. Cheliceral teeth are also named according to Muma (1951), where sizes of cheliceral teeth are ordered with Roman numerals, and size I is larger than II and so on. The tarsal spination is represented as in Roewer (1934), Muma (1951) and Maury (1970). The term "ctenidia" is used as in Maury (1984). Type material is deposited in Museu de Zoologia da Universidade de São Paulo (MZUSP), State of São Paulo, Brazil.

The study was carried out on Ibiraba—sand dunes on the northeastern Brazilian caatinga (Fig. 1). The vegetation physiognomy is described in Rocha (1991). There is a large

amount of exposed sandy soil. Nimer (1979) reported an annual mean precipitation of 692 mm. There are two distinct seasons, a dry season from April–September and a rainy season from October–April.

A grid with 128 pitfall traps covered two dune summits and two valleys during February, and a similar one with 120 traps was set in September 1996. Each trap consisted of a plastic cylindrical receptacle (30 × 40 cm) to which three drift fences (Corn 1994) 1.5 m long were radially attached. The distance between traps was 7 m. No chemicals or baits were used in the traps. The microhabitat around each trap was recorded once each month as seven variables: microgeographic position (summit, talude, plateau or valley), vegetation covering (cm² inside a 3.0 m diameter circle centered in each trap) by trees, shrubs, subshrubs, *Bromelia antiacantha* (Bromeliaceae), *Opuntia inamoena* (Cactaceae) and litter cover. The pitfalls were scanned for solpugids twice a day, around 0600 h and 1700 h. Comparing three methods of collecting solifuges, Muma (1980) suggested pitfall trapping as the most suitable method for number of individuals and species composition estimates. Pitfalls were also used

by Griffin (1990) in the Namibia desert to study microhabitat preferences, species richness and activity patterns.

For spatial distribution pattern analysis, Morisita's index of dispersion (Id) was applied and its departure from the unity was evaluated by a chi-square test (Brower et al. 1997). The analysis on preferemces by the solpugid on each microhabitat variable on ratio scale was carried out using Mann-Whitney U-test comparing the distribution of the values of each variable by the event of capture with the distribution of the same variable obtained on the entire sampling grid. Habitat preference on the cathegoric variable microgeographic position was checked using the goodness of fit test.

Family Mummuciidae

Mummucia mauryi new species Rocha

Types.—Holotype male, MZUSP 16470 (col. P. Rocha, 26 February 1996). Paratypes: 1♂1♀ MZUSP 15784 and 2♀ MZUSP 15932 (col. E. Xavier, February 1996); 1♂ MZUSP 16471 and 2♂ MZUSP 16472 (col. P. Rocha, 25 February 1996); 1♂ MZUSP 16473 (col. E. Xavier, 11 December 1996); 1♂ MZUSP 16474 (col. E. Xavier, 12 December 1996). All from Ibiraba, western side of São Francisco River, State of Bahia, Brazil. 10°48′S, 42°50′W.

Etymology.—The specific name is given in honor to the late Dr. Emilio Maury.

Diagnosis.—*Mummucia mauryi* is a species of Mummuciidae whose anterior tooth of the movable finger is smaller than the intermediate tooth in males and similar to intermediate in females.

Description.—*Male:* Coloration in 80% ethanol: Prosoma. Propeltidium white, central portion brown, dark brown near the lateral lobe grooves. Ocular tubercle black, with a longitudinal white narrow stripe between the eyes. Peltidium white, posterior border brown. Parapeltidium, mesopeltidium and metapeltidium similar to opisthosomal tergites. Chelicerae pale brown, three longitudinal white stripes on ectal face joined dorsally above the fondal teeth. Pedipalpi and legs brown, ventral face pale brown. Malleoli pale brown with small brown spots on distal border (Fig. 5). Opisthosoma: Lateral borders of tergites white, with wide dark brown stripe on the central half, which is darker near the posterior

border of the tergites. Brown bifid setae with brown sockets when they are in white area of the tergites, and white sockets when in the dark brown area. Pleurites (Fig. 6) white, dorsal portion dark brown. Pale brown translucent bifid bristles in the white portion have sockets shaped into dark brown spots, which are generally arranged as in Fig. 6. Sternites pale brown, lateral posterior borders brown in the four distal. First to fourth post-spiracular sternites with brown spots which include the sockets of some bifid bristles. All covering bristles and bifid bristles are translucent pale brown. *Morphology and chaetotaxy:* Prosoma: Propeltidium with some scattered bifid setae, slightly wider than long (Table 1) and separated from lateral lobes by dorsal grooves. Ocular tubercle prominent with bifid setae anteriorly oriented. Distance between two eyes about twice eye diameter. Peltidium narrow, with a transverse row of bifid setae. Parapeltidium smooth. Mesopeltidium wider than long, semicircle-shaped, with several bifid setae in the posterior border. Metapeltidium wider than long, with several bifid setae. Chelicerae (Figs. 2, 3): stridulatory apparatus on mesal face with seven parallel narrow grooves; ectal face with several short bristles and several setae, bifid or acuminate; movable finger with one anterior, one intermediate and one principal tooth, graded in size from distal to proximal III, II, I; fixed finger dentition: two anterior teeth (the first one may be vestigial), one intermediate and one principal tooth, graded in size from distal to proximal II, I, IV, III; five ectal fondal teeth, graded in size, from distal to proximal I, II, III, II, II (the 5th may be absent); three mesal fondal teeth, graded in size from distal to proximal I, II, II, the first distal separated from the others by a diastema; in the center of the dorsal face the fixed finger bears one very long seta (about the length of femur IV) with a prominent socket; flagellum (Figs. 2, 10) thin, translucent drop-shaped vesicle, laterally flattened and with a longitudinal ectal opening (in the face adjacent to the chelicera), which extends from near the attachment base to the tip of the flagellum. The attachment base of the flagellum is a sclerotized ring placed posteriorly in its ectal face. Pedipalp: tarsi immovable, without spines, densely covered by differentially sized bifid bristles, with some very long setae in metatarsi and tibiae (about twice the length
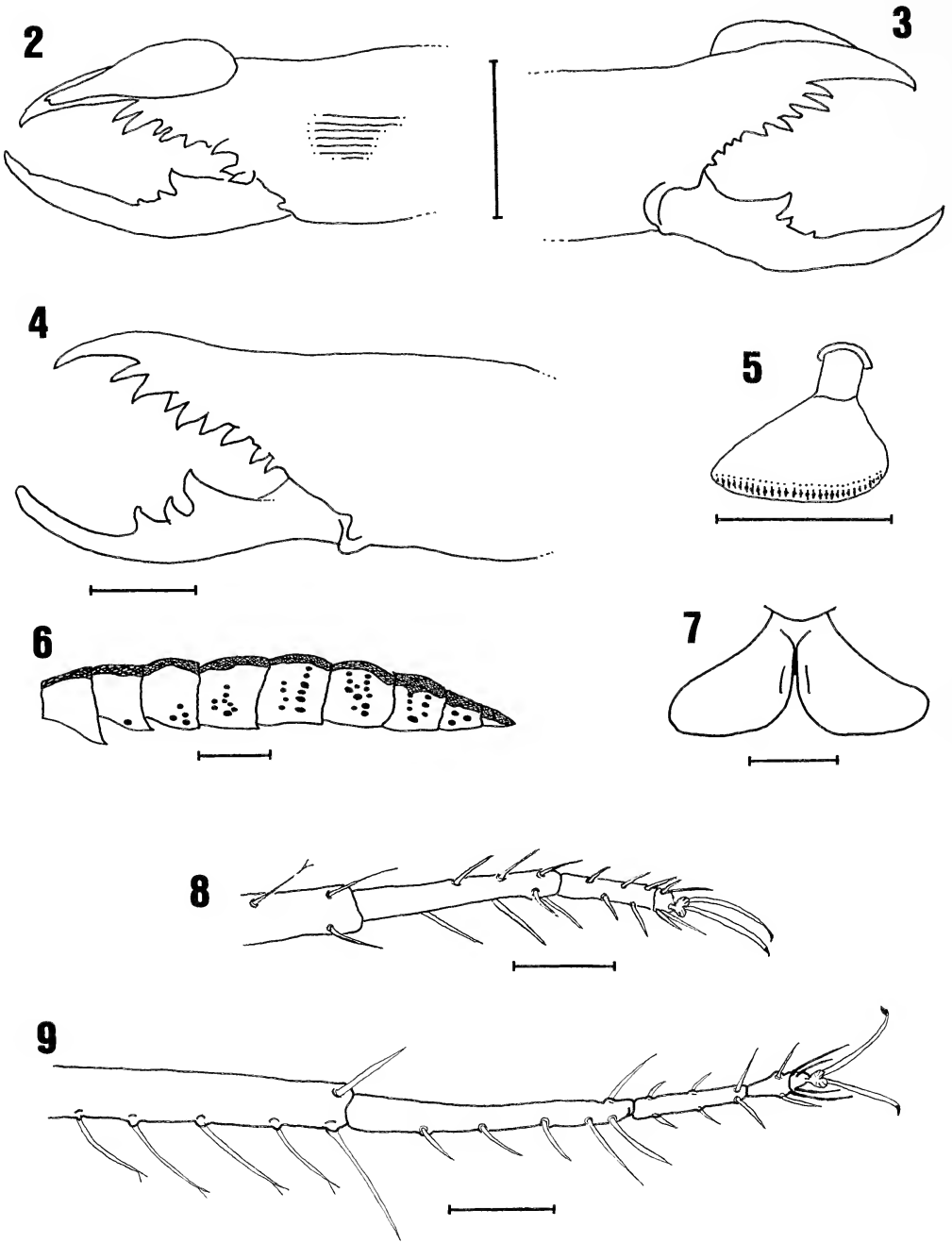
Figures 2–9.—*Mummucia mauryi* new species. 2. Male right chelicera, mesal view; 3. Male right chelicera, ectal view; 4. Female left chelicera, ectal view; 5. Male right malleolus V; 6. Male left pleurites; 7. Female genital sternite; 8. Female left leg III; 9. Male right leg IV.

of pedipalpal tibia). Legs: with several differentially-sized bifid bristles and some bifid setae. Some very long setae in dorsal surface (about twice the length of metatarsus IV). Leg I thin, without claws and spines. Legs II and III (see female leg III, Fig. 8): tibiae with 1 or 1.1 ventral bifid spines and a distal pair of ventral spines; metatarsus with three retrolateral spines and 1.1.2 ventral spines; tarsi two-segmented with 1.2.2/1.2 or 1.2.2/2.2 ventral

Table 1.—Morphometric characters of **Mummucia mauryi** new species. Measurements are in millimeters (except propeltidium length/width ratio) and were recorded as described in Muma (1951).

Morphometric character	Male holotype (MZUSP 16470)	Range among males (7 individuals)	Female paratype (MZUSP 15932)	Range among females (3 individuals)
Total length	7.55	7.10–8.10	11.20	8.55–11.20
Cheliceral length	1.71	1.70–1.80	2.60	1.75–2.60
Cheliceral width	0.50	0.50–0.61	0.88	0.60–0.88
Propeltidium length	1.15	1.11–1.30	1.47	0.99–1.47
Propeltidium width	1.35	1.32–1.40	2.05	1.35–2.05
Propeltidium length/ width ratio	0.85	0.84–0.93	0.72	0.71–0.73
Pedipalp	4.80	4.45–4.90	5.70	3.90–5.70
Leg I	4.00	3.20–4.20	4.90	3.40–4.90
Leg IV	7.40	6.20–8.40	9.50	5.50–9.50

spines. Leg IV (Fig. 9): tibia with an anterior row of 1.1.1.1 ventral bifid spines and a distal pair of ventral spines; metatarsus with 1.1.1.1.2 ventral spines; tarsi three-segmented, with 2.2.2/2/1.2 or 2.2.2/2/2.2 ventral spines. Malleoli as in Fig. 5. Opisthosoma: Tergites wider than long, with rounded borders, covered by bifid setae and bifid bristles. Sternites wider than long, densely covered by bifid bristles. Genital operculum with central longitudinal opening. Posterior border of 2nd post-spiracular sternite with a row of about 50 ctenidia, more rigid and slightly longer than the bifid bristles in sternites. Morphometric characters in Table 1.

Female: Similar to male, but with the following particular features. Coloration in ethanol 80% similar to male, but with lighter tonalities. *Morphology and chaetotaxy:* Prosoma: Propeltidium wider than long with numerous bifid setae and small bifid bristles. Eyes separated by three times the eye diameter. Chelicerae (Fig. 4): movable finger with one anterior, one intermediate and one principal tooth graded in size from distal to proximal II, II, I. Fixed finger with two anterior teeth, one intermediate and one principal, graded in size from distal to proximal I, I, III, II (the first anterior may be slightly smaller than the 2nd). Five ectal fondal teeth graded in size from distal to proximal I, I, IV, II, III (the 3rd may be vestigial). Mesal fondal teeth as in male. Leg III similar to male (Fig. 8). Leg IV: tibia with an anterior row of 1.1.1 or 1.1.1.1 ventral bifid spines and a distal pair of ventral spines; metatarsus with 1.1.2 or 1.1.1.2 ventral spines. Opisthosoma. Sternites densely and

uniformly covered by bifid bristles, without conspicuous sockets. Genital operculum prominent, fan-shaped, round-bordered, with central longitudinal opening (Fig. 7). Posterior border of 2nd post-spiracular sternite with a row with several ctenidia, slightly longer than the bifid bristles of the sternites. Morphometric characters in Table 1.

Systematic comments.—There is no consensus about the number and the systematic position of genera of the family Mummuciidae. For instance, Muma (1976) recognizes 11 genera in Mummuciidae (six of them monotypic), whereas Maury (1984) has transferred three of these genera to the family Ammotrechidae. The typical genus *Mummucia* Simon 1879 has only three species, which are known only by females (Muma 1976) and one of them (*Mummucia patagonica* Roewer 1934) should be transferred to family Ammotrechidae, since this species bears spines at the pedipalpal metatarsi, a distinctive character of this family. According to Maury (pers. comm. 30 December 1997, 1998), there is no good character to distinguish the genera of Mummuciidae, so that the most conservative decision is to consider the new Mummuciidae species herein described as belonging to the typical genus *Mummucia*, until more precise information about the taxonomy and phylogeny of the group become available.

The shape of the flagellum is a good character for the definition of Neotropical families and in Mummuciidae the flagellum is vesicular (Maury 1984). The flagellum of *M. mauryi* new species bears a longitudinal ectal opening, which has not been reported in other
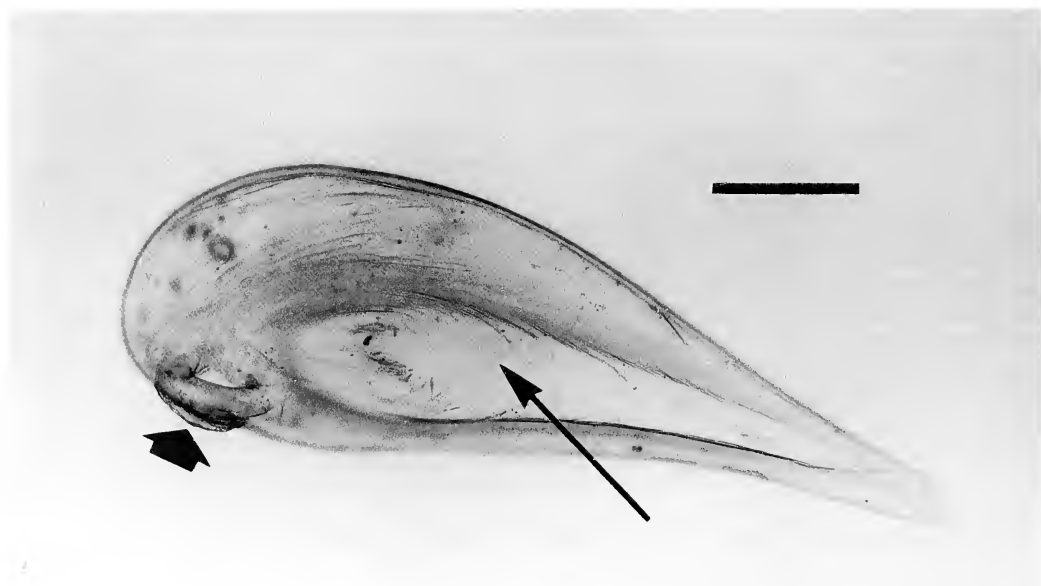
Figure 10.—Photomicrograph of the flagellum of *Mummucia mauryi* new species, showing the longitudinal lateral opening in the face adjacent to chelicerae, indicated by the long arrow. The short arrow indicates the attaching ring. Scale = 0.1 mm.

Mummuciidae species. Therefore this character may be useful in further studies on the systematics of Mummuciidae.

AUTOECOLOGY

Specimens of *Mummucia mauryi* new species represented 5% of all arachnid specimens collected by the pitfall trap method described above (Xavier & Rocha 1998): 22 specimens were collected in February (rainy season) and 88 in September (dry season). The traps examined during the morning showed no solifuges. This agrees with Maury (1984), who predicted that mummuciids should be the only South American solifuges with diurnal habits. Indeed, Cloudsley-Thompson (1977, 1978) suggested that *Mummucia variegata* (Gervais) 1849 is a diurnal species, and that diurnal activity is exhibited by smaller and brightly-colored solpugid species. On the other hand, Wharton (1987) states that "there are several large, diurnal solifuge species in the arid regions of southern Africa." *Mummucia mauryi* new species agrees with both Cloudsley-Thompson and Maury predictions, being a brightly-colored, small and diurnal mummuciid species. Because solifuges are "unusually tolerant of high temperature (. . .) and have

very low transpiration rates (. . .), it seems probable that the avoidance of predators may be of greater significance than thermal physiological requirements in their night-active behavior" (Cloudsley-Thompson 1991). Following this idea, we should expect diurnal solifuges to exhibit additional mechanisms of predator avoidance.

As discussed below, the analyses performed detected preferences only twice for microhabitat variables and once for microgeographic region. There was detected a positive preference for areas covered by *Opuntia inamoena* (Cactaceae) during the dry season ($U = 4592$, $P = 0.03$). The African solpugid *Lipophaga trispinosa* Purcell 1903 is restricted to low plant cover areas during dry periods (Dean & Griffin 1993). They also found a low diversity of solifuges associated with loose sand soil. For *Eremobates marathoni* Muma 1951, Punzo (1998) detected a preference for sandy soils, open areas and scattered clumps of vegetation, and he suggested that "scattered clumps of vegetation afford cover and protection from predators (. . .) including night hawks, roadrunners, scorpions, and other solifuges." In fact, *Opuntia inamoena* is an in-

hospitable spiny plant, which may be avoided by many possible predators such as diurnal birds. Nevertheless, a parallel study on lizards at the same area was carried out by Rocha (1998) showing preference for *O. inamoena* by the lizard *Tropidurus psammonastes* (Tropiduridae). The lizard's diet includes mainly ants and insect larvae, and solifuges are rarely preyed on, as one only event was recorded.

"The avoidance of open areas devoid of vegetation appears to be a rather common trait in solifuges" (Punzo 1998). This seems to be the case to *Mummucia mauryi* new species. During the dry season it showed a negative preference for dune summits ($\chi^2 = 9.74$, $0.025 < P < 0.05$) and areas covered by heliophylic subshrubs ($U = 4212$, $P = 0.009$), which is here interpreted as avoidance of sun-exposed areas, which may be associated with avoidance of predators and/or environmental extremes.

Morisita's index was 3.32 ($\chi^2 = 175.818$, $0.005 > P > 0.001$) in the rainy season and 1.38 ($\chi^2 = 151.209$, $0.025 > P > 0.01$) in the dry season, indicating a clumped distribution through the year. Investigating the eremobatid solifuge *Eremobates palpisetulosus* Fichter 1941, Punzo (1997) found a clumped dispersion pattern, without significant differences in adult dispersion as a function of sex or season.

ACKNOWLEDGMENTS

LITERATURE CITED

Brower, J.E., J.H. Zar & C. Von Ende. 1997. Field and Laboratory Methods For General Ecology. McGraw-Hill. New York.

Cloudsley-Thompson, J.L. 1977. Adaptational biology of Solifugae (Solpugida). Bulletin of the British Arachnological Society 4(2):61–71.

Cloudsley-Thompson, J.L. 1978. Biological clocks in Arachnida. Bulletin of the British Arachnological Society 4(4):184–191.

Cloudsley-Thompson, J.L. 1991. Ecophysiology of Desert Arthropods and Reptiles. Springer-Verlag, Berlin.

Corn, P.S. 1994. Straight-line drift fences and pitfall traps. P. 109. *In* Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. (W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek & M.S. Foster (eds.). Smithsonian Inst. Press, London.

Dean, W.R.J. & E. Griffin. 1993. Seasonal activity patterns and habitats in Solifugae (Arachnida) in southern Karoo. South African Journal of Zoology 28:91–94.

Griffin, E. 1990. Seasonal activity, habitat selection and species richness of Solifugae (Arachnida) on the gravel plains of the central Namib Desert. Transvaal Museum Monograph 7:77–82.

Höfer, H. & L. Beck. 1995. Die Spinnentierfauna des Regenwaldreservats "Reserva Ducke" in Zentralamazonien I. Natur und Museum 125(12): 389–401.

Maury, E.A. 1970. Sobre la presencia de *Gaucha fasciata* Mello-Leitão 1924 en la Argentina. Physis 79(29):357–362.

Maury, E.A. 1982. Solífugos de Colombia y Venezuela (Solifugae, Ammotrechidae). Journal of Arachnology 10(2):123–143.

Maury, E.A. 1998. Solifugae. Pp. 560-568. *In* Biodiversdidad de Artropodos Argentinos. (J.J. Morrone & S. Coscarón, eds.). Ediciones SUR. La Plata.

Maury, E.A. 1984. Las familias de solífugos americanos y su distribución geográfica (Arachnida, Solifugae). Physis C. 42(103):73–80.

Mello-Leitão, C. 1924. A new South-American solpugid. Revista Chilena de Historia Natural XXVIII:140–143.

Muma, M.H. 1951. The arachnid order Solpugida in the United States. Bulletin of the American Museum of Natural History XCVII(2):35–141.

Muma, M.H. 1980. Comparison of three methods for estimating solpugid (Arachnida) populations. Journal of Arachnology 8:267–270.

Nimer, E. 1979. Climatologia do Brasil. Rio de Janeiro, IBGE, 421 pp.

Punzo, F. 1997. Dispersion, temporal patterns of activity and phenology of feeding and mating behavior in *Eremobates palpisetulosus* (Solifugae, Eremobatidae). Bulletin of the British Arachnological Society 10:303–307.

Punzo, F. 1998. The Biology Of Camel Spiders (Arachnida, Solifugae). Kluwer Academic Publishers.

Rocha, L.S. & E.M. Cancello. 1997. A ordem Solifugae na América do Sul: novas perspectivas para o seu conhecimento. P. 50. *In* Actas del Primer Encuentro de Aracnologos del Cono Sur.

(M. Simó, ed.) 1 a 5 Diciembre 1997. Facultad de Ciencias/ I. NA. PE. Montevideo, Uruguay.

Rocha, P.L.B. 1991. Ecologia e Morfologia de Uma Nova Espécie de *Proechimys* (Rodentia: Echimidae) das Dunas Interiores do Rio São Francisco, Bahia. M.S. thesis, University of São Paulo, São Paulo, Brazil.

Rocha, P.L.B. 1998. Uso e Partição de Recursos Pelas Espécies de Lagartos Das Dunas do Rio São Francisco, Bahia (Squamata). Ph.D. thesis, University of São Paulo, São Paulo, Brazil.

Roewer, C.F. 1934. Solifugae, Palpigradi. Pp. 461–608, *In* Klassen und Ordungen des Tierreichs. (H.G. Bronns, ed.). vol 5, div. 4, book 4. Leipzig.

Roewer, C.F. 1954. Einige neue Opiliones Laniatores und Solifugae. Abhandlungen Natur-wissenschaftlichen Verein Zu Bremen 33(3): 377–384.

Savory, T.H. 1964. The order Solifugae. Pp. 184–193. *In* Arachnida. (W. & J. Mackay, eds.). Academic Press, London.

Wharton, R.A. 1987. Biology of the diurnal *Metasolpuga picta* (Kraepelin) (Solifugae, Solpugidae) compared with that of nocturnal species. Journal of Arachnology 14:363–383.

Xavier, E. & P.L.B. Rocha. 1998. Microhabitat use by an assemblage of cursorial arachnids in sand dunes from Brazilian semiarid caatinga. XIV International Congress of Arachnology American Arachnological Society (abstract).

AN UNUSUAL NEW SPECIES OF *MUNDOCHTHONIUS* FROM A CAVE IN COLORADO, WITH COMMENTS ON *MUNDOCHTHONIUS MONTANUS* (PSEUDOSCORPIONES, CHTHONIIDAE)

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ABSTRACT. *Mundochthonius singularis*, a troglomorphic species from Fly Cave in Fremont County, Colorado, is described. This is the first cavernicolous pseudoscorpion to be reported from the state. It is compared with *M. montanus*, the local epigean species, for which an emended description is given.

Keywords: Pseudoscorpiones, Chthoniidae, *Mundochthonius*, cavernicole, Colorado

The genus *Mundochthonius* Chamberlin 1929 is Holarctic in distribution, with two species known from subtropical areas, in Mexico and Hispaniola (see references in Harvey 1991). Its member species are mostly very small, litter-dwelling creatures; and some have been found in caves. In the United States eight species have been described, two of which are cavernicolous, namely, *Mundochthonius cavernicola* Muchmore 1968 from Illinois and *M. holsingeri* Benedict & Malcolm 1974 from Virginia. Recently, another cavernicolous species has been discovered in Colorado, this one more highly troglomorphic than the other two; it is described below. But first, I take this opportunity to redescribe *Mundochthonius montanus* Chamberlin 1929, the surface-dwelling species in the area, for comparison with the new cave-dwelling form.

The specimens studied here have been dissected, cleared, and mounted in Canada balsam on microscope slides. They are in the following depositories: California Academy of Sciences, San Francisco, California (CAS); Florida State Collection of Arthropods, Gainesville, Florida (FSCA). Some abbreviations are used in the descriptions: L = length; L/B = ratio, length/breadth; L/D = ratio, length/depth; m = microseta; T = tactile seta.

Genus *Mundochthonius* Chamberlin

Mundochthonius Chamberlin 1929: 64; Beier 1932: 36; Hoff 1949: 436; Hoff 1956: 10; Morikawa 1960: 94; Beier 1963: 18; Muchmore 1973: 48; Benedict 1978: 250; Harvey 1991: 190.

Though not reported here in detail, the holotype male of *Mundochthonius erosidens* Chamberlin 1929, type species of *Mundochthonius*, has been examined and found to support the following diagnosis.

Diagnosis.—*Mundochthonius* is easily diagnosed. It shares the following characters with several other chthoniid genera, namely, *Austrochthonius* Chamberlin 1929, *Congochthonius* Beier 1959, *Francochthonius* Vitali-di Castri 1976, *Malcolmochthonius* Benedict 1978, and *Mexichthonius* Muchmore 1975: 1) coxal spines present only on coxae II; 2) contiguous teeth on fingers of palpal chela; 3) trichobothrium *sb* (usually much) closer to *st* than to *b* on movable chelal finger; 4) epistome prominent, serrate; 5) one or more microsetae on anteromedial process (apex) of coxa I. However, it may be distinguished from all of these by the possession of a bisetose intercoxal tubercle between the bases of coxae III and IV.

Remarks.—Though not mentioned by Chamberlin (1929), the holotype of *Mundochthonius erosidens* has a small, but distinct, heavily serrate, triangular epistome at the middle of the anterior margin of the carapace. All other species in the genus appear to have a similar, but usually larger, epistome.

American species of *Mundochthonius* (including *M. erosidens*) appear to have only two weak eyes or none at all. On the other hand,

one species in Europe, *M. alpinus* Beier 1947 (and 1963), is described as having four eyes, though other species in Europe and Asia are reported to have only two eyes or none (see references in Harvey 1991).

Contrary to the statement of Chamberlin in his "Analytical Key to the Genera of the Kewochthonini" (1929: 63), all American species of *Mundochthonius* that I have examined (including *M. erosidens*) possess 1–3 microsetae on the anteromedial process (apex) of coxa I. Species from elsewhere are also reported to possess these small setae.

The coxal spines of the American species of *Mundochthonius* that I have examined appear as flattened blades, variously indented or incised at the distal ends and along the sides, as described and figured by Chamberlin (1929, 1931), by Hoff (1949, 1952), and by Muchmore (1973). None looks like the cone-shaped, setaceous or spiny structures described and illustrated for *M. alpinus* Beier (1947, 1963), and for *M. decoui* Dumitresco & Orghidan (1970), or those of *M. carpaticus* Rafalski (1948); nor do they appear as thick and lobe-like as those of *M. basarukini* Schawaller (1989). Because of the minute size of the coxal spines in most species of *Mundochthonius*, satisfactory descriptions of their structure will probably be achieved only by following Schawaller (1989) in the use of scanning electron microscopy. In any event, the "coxal spines" of the new species, *M. singularis*, are unique in being very deeply dissected and elongated to resemble, somewhat, the antlers of a deer.

Mundochthonius montanus Chamberlin
Figs. 1, 2, 8

Mundochthonius montanus Chamberlin 1929: 65; Chamberlin 1931: fig. 21I; Hoff 1952: 40, figs. 1–4; Hoff 1956: 10; Hoff 1959: 26, 33, etc.; Hoff 1961: 420; Harvey 1991: 191.

Type data.—Holotype female (JC-86.01001) from "Manitou [El Paso County] - Colorado. Elev. 8500. In - soil (surface). Coll. E.W. Goldsmith." (mounted on microscope slide by J.C. Chamberlin; in CAS, Type No. 17445).

The original description by Chamberlin (1929) was very brief. Hoff (1952, 1956, 1961) added some observations and measurements based on specimens from New Mexico and Colorado, but he did not record several

important details. It seems wise to redescribe the holotype in relation to Hoff's material, in order to firmly establish the species. The holotype has been dissected, the body stained pink, and mounted in Canada balsam; the right palp is missing and the left palpal segments have been somewhat compressed and broken by the cover; many vestitural setae are too faint to see clearly.

Redescription of holotype female.—Representative of the genus as outlined above and with the following particular features. Carapace a little longer than broad; epistome small, triangular, serrate; two very small eyes; chaetotaxy 6-4-4-2-2. Coxal area typical, but no microsetae observable on apex of coxa I; coxal spines as shown by Chamberlin (1931: fig. 21I); bisetose intercoxal tubercle present. Tergal chaetotaxy 4:4:6:6:6:6:-(others not observable). Sternal chaetotaxy 10:(3)8(3):-(others not observable). Chelicera about 0.85 as long as carapace; flagellum of nine setae; spinneret a small knob on finger margin; setae on hand not observable, but Chamberlin reported six (1929: 64). Palp rather robust (see Fig. 1). Because of damage, the palpal segments are not measurable with accuracy; Chamberlin reported L/B of femur and chela as 4 and 3.8, respectively. Measurements and ratios for some other Colorado specimens are given below. Trichobothriotaxy typical (see Fig. 2). Chelal fingers with numerous but not countable, small, contiguous teeth. Leg IV rather robust (see Fig. 8): L/D of femur+patella 2.45, tibia 3.15.

Measurements (mm).—(These given are deemed reliable in spite of some distortion of the body parts). Body L 1.00. Carapace L 0.33. Chelicera L 0.295. Palp: femur 0.31/?; patella 0.155/?; chela 0.495/?; hand 0.185/?; movable finger L 0.34. Leg IV: femur+patella 0.26/0.115; tibia 0.19/0.06.

Variation.—As discussed by Hoff (1961), there is considerable variation among the specimens assigned to *Mundochthonius montanus*. According to the values given by Hoff (1952, 1961), the measurements for *M. montanus* in New Mexico and Colorado range as follows (females average slightly larger than males): Body L 0.92–1.25. Carapace L 0.32–0.40. Palpal femur 0.263–0.350/0.068–0.094; patella (New Mexico only) 0.155–0.186/0.086–0.105; chela 0.420–0.545/0.100–0.127; hand 0.155–0.211/0.100–0.126; movable fin-
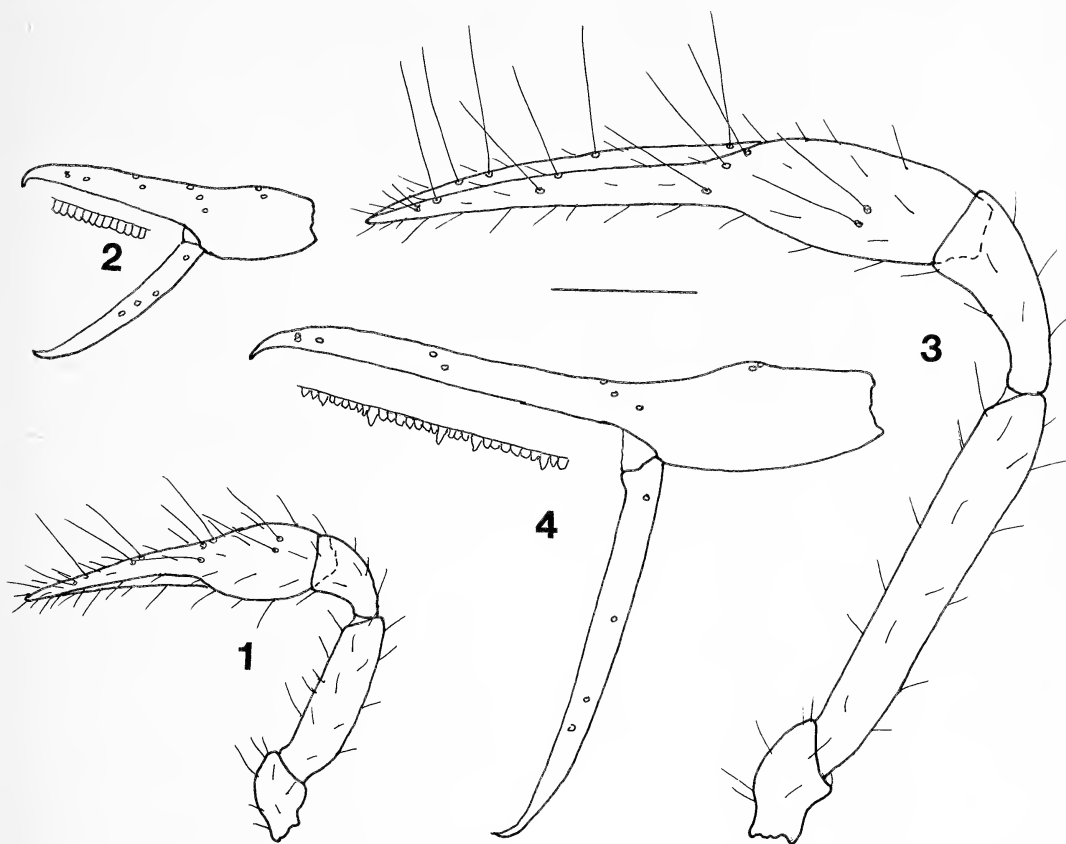
Figures 1–4.—Species of *Mundochthonius*, palps. Figs. 1, 2. *Mundochthonius montanus* Chamberlin, female from Colorado. 1. Right palp, dorsal view; 2. Left chela, lateral view, setae omitted, with teeth from fixed finger. Figs. 3, 4. ***Mundochthonius singularis*** new species, holotype female. 3. Right palp, dorsal view; 4. Left chela, lateral view, setae omitted, with teeth from fixed finger. Scale = 0.25 mm.

ger L 0.270–0.355. Ratios of palpal segments: L/B of femur 3.3–3.9, patella 1.65–1.85, and chela 3.85–4.5; L/D of hand 1.4–1.65; movable finger 1.7–1.85× as long as hand. All the reliable measurements and ratios of the holotype fall well within these ranges.

No microsetae (m) are visible on anteromedial process of coxa I of the holotype, probably because of long exposure to clearing agent. However, two or three such setae do appear on coxa I of all other specimens of *M. montanus* I have examined from Colorado and New Mexico.

The coxal spines are quite varied in shape, from a single broad, incised blade, as figured by Chamberlin for the holotype (1931: fig. 21I), to two or three separate, narrower, incised or dentate blades (Hoff 1952: figs. 1–4; 1961: 421).

There are about 50 marginal teeth on each finger of the palpal chela. They are contiguous

basally, uniform in height, and slightly retrodentate or rounded (Fig. 2).

Remarks.—*Mundochthonius montanus* is a generalized, epigean species, apparently common in the Rocky Mountains of Colorado and New Mexico. According to Hoff (1959, 1961), it is adapted to life in a wide variety of litter and decomposing wood of logs and stumps, at elevations of 6900–11,000 feet (2100–3350 m). Presumably, it represents the population from which the specialized, cavernicolous *M. singularis* was derived.

Mundochthonius singularis new species
Figs. 3–7

Type data.—Holotype female (WM8097. 01001) from under a rock, about 30 m inside Fly Cave, 20 km N of Canon City, Fremont County, Colorado (see Parris 1973: 89–90), 7 August 1996, P. Beron (slide, in FSCA).

Diagnosis.—Differs from other species of
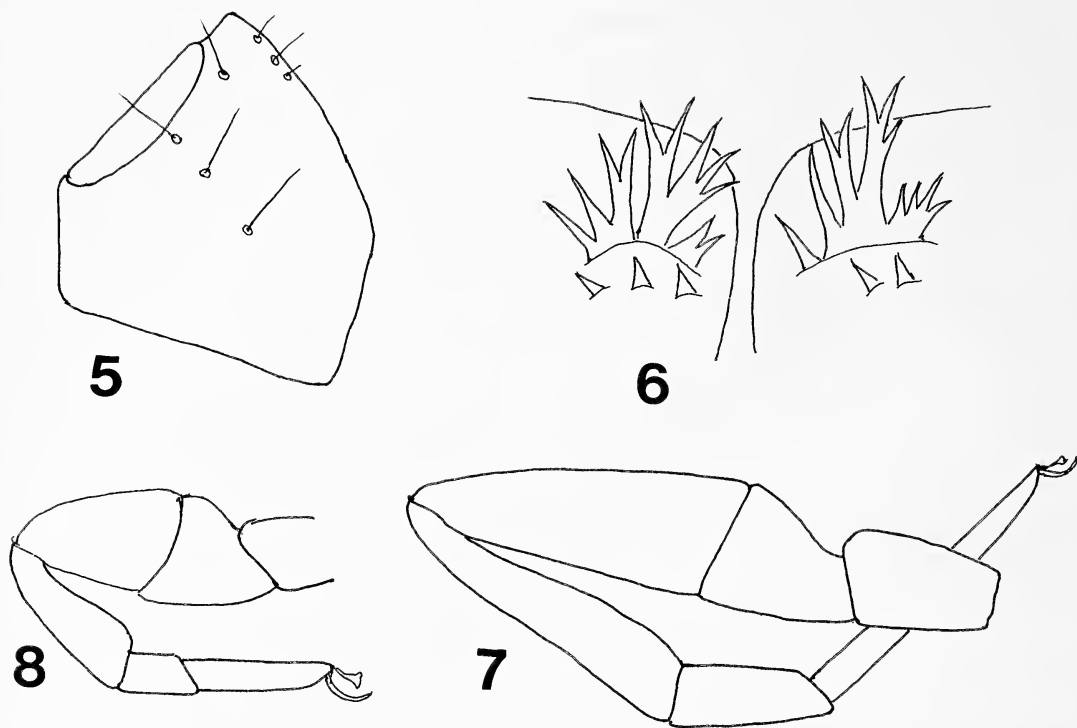
Figures 5–8.—Species of *Mundochthonius*, various features. Figures 5–7. ***Mundochthonius singularis*** new species, holotype female. 5. Right coxa I (ventral view), showing microsetae on apex; 6. Coxal spines on coxae II (ventral view); 7. Leg IV, setae omitted. 8. *Mundochthonius montanus* Chamberlin, female from Colorado: Leg IV, setae omitted.

the genus in its troglomorphic adaptations: large size (palpal chela 1.07 mm long), attenuated appendages (L/B of palpal chela = 5.8), and an unique arrangement of coxal spines; also, the palpal chelae are heterodentate, rather than homodentate as seen in other species of the genus.

Description.—With the characters of the genus as outlined above, and the following particular features. Chelicerae and palps light brown, carapace tan, other parts lighter. Carapace about as long as broad, narrowed posteriorly; epistome large, irregularly serrate; no eyes; chaetotaxy 6-4-4-2-2. Coxal area generally typical; chaetotaxy 2-2-1:2or3m-2-2(1): 2-4(3)-CS:2-5(4):2-3; each coxa I with 2–3 microsetae (m) on medial edge of apex (Fig. 5); each coxa II with an unusual complex of coxal spines (CS), consisting of several differently shaped elements, one on each side somewhat resembling an antler of a deer (Fig. 6); a bisetose intercoxal tubercle present. Tergal chaetotaxy 4:4:4:6:6:6:6:6:6:6:1T2T1:0; sternal chaetotaxy 10:(4)6(4):(2)6(2):11:10:9:

10:8:7:0:2. Chelicera 0.85 as long as carapace; hand with 6 setae; flagellum of 10 setae; galea a very small elevation; each finger with 10–15 small teeth. Palp long and slender (Fig. 3); femur 1.45× and chela 2.05× as long as carapace. L/B of trochanter 1.75, femur 6.25, patella 2.35, and chela 5.8; L/D of hand 2.1; movable finger 1.8× as long as hand. Surfaces smooth. Trichobothria as shown in Fig. 4. Fixed finger with about 95 and movable finger with about 85 contiguous, cusped teeth; on each finger, about 12 teeth are conspicuously larger and sharper than adjacent ones (Fig. 4). Legs long and slender: leg I with femur 2.05× as long as patella; leg IV (Fig. 7) with L/D of femur+patella 3.8 and tibia 4.8.

Measurements (mm).—Holotype female (male unknown). Body L 1.59. Carapace L 0.52. Chelicera L 0.45. Palp: trochanter 0.22/ 0.125; femur 0.75/0.12; patella 0.355/0.15; chela 1.07/0.185; hand 0.385/0.185; movable finger L 0.69. Leg I: femur 0.38/0.06; patella 0.185/0.06. Leg IV: femur+patella 0.53/0.14;

tibia 0.385/0.08; basitarsus 0.18/0.06; telotarsus 0.355/0.045.

Etymology.—The species is called *singularis* (Latin, *different*) for its unusual characters, especially the coxal spines, compared with other members of the genus.

Remarks.—*Mundochthonius singularis* is the first cavernicolous pseudoscorpion recorded from Colorado. It is certainly troglobitic, being much more highly modified for cave life than any other known species of the genus. It is the largest known species of *Mundochthonius*, with lengths of palpal femur and chela 0.75 and 1.07 mm respectively, compared to the cavernicolous *M. cavernicola* (0.57 and 0.92 mm) and the epigean *M. montanus* (0.26–0.35 and 0.44–0.54 mm); and it has very slender appendages, with L/B of palpal femur and chela 6.25 and 5.8, compared to *M. cavernicola* (4.4 and 4.65) and *M. montanus* (3.5–4.0 and 3.8–4.35). Correlated with the elongated chela, trichobothrium *sb* on the movable finger is much farther removed from *st* than it is in other species of the genus; but it is still closer to *st* than to *b*.

The coxal spines are uniquely deeply incised and enlarged, apparently an adaptation to some aspect of life in a cave. The coxal spines of the other known cavernicolous species, *M. cavernicola* and *M. holsingeri*, are not so modified. The function of the coxal spines of chthonioid pseudoscorpions is not known with certainty, but Chamberlin (1931: 93) considered it "most probable that they are sensory, perhaps tactile." Alternatively, Judson (1990) reported observations of the coxal spines of three species of chthonioids from West Africa being used in cleaning the legs. Whether one or both of these functions is operative in *Mundochthonius* is still unknown.

In *Mundochthonius montanus* and other species in the genus, the palpal chelae may be characterized as "homodentate"—adjacent teeth of the marginal rows are very much alike, and any differences in size and shape tend to be gradual along the row. In *M. singularis*, however, there are frequent teeth which are distinctly broader and taller than adjacent teeth. It may be supposed that this unusual dentition is correlated with a diet in the cave different from that of the other species.

Fly Cave is named for the many flies encountered just inside the entrance (Pollard 1954; Parris 1973). According to Ayre

(1961a, b), the flies are *Neomuscina tripunctata* (Van der Welp), "a breed common in Mexico and rang[ing] into this portion of the state of Colorado." Also, Fly Cave is the type locality of the unusual spider *Hypochilus bonneti* Gertsch 1964 (and see Vogel & Ayre 1961). Neither the fly nor the spider is troglobitic.

ACKNOWLEDGMENTS

LITERATURE CITED

Ayre, R.W. 1961a. Bats and bugs. Caving in the Rockies, Colorado Grotto, National Speleological Society 7:1–3.

Ayre, R.W. 1961b. From the biology notebook. Caving in the Rockies, Colorado Grotto, National Speleological Society 7:13.

Beier, M. 1932. Pseudoscorpionidea I. Subord. Chthoniinea et Neobisiinea. Das Tierreich 57:1–258.

Beier, M. 1947. Neue Pseudoscorpione aus der Steiermark. Annalen des Naturhistorischen Museum in Wien 55:296–301.

Beier, M. 1959. Pseudoscorpione aus dem Belgischen Congo gesammelt von Herrn N. Leleup. Annales du Musée Royal du Congo Belge, Tervuren, Sciences Zoologiques 72:5–69.

Beier, M. 1963. Ordnung Pseudoscorpionidea (Afterskorpione). *In* Bestimmungsbücher zur Bodenfauna Europas. Akademie-Verlag, Berlin 1:1–313.

Beier, M. 1971. Ein neuer *Mundochthonius* (Arachnida, Pseudoscorpionidea) aus der Steiermark. Mitteilungen des Naturwissenschaftlichen Vereins für Steiermark 100:386–387.

Benedict, E.M. 1978. A new pseudoscorpion genus *Malcolmochthonius* n. g., with three new species from the western United States. Transactions of the American Microscopical Society 97:250–255.

Benedict, E.M. & D.R. Malcolm. 1974. A new cavernicolous species of *Mundochthonius* from the eastern United States (Pseudoscorpionida, Chthoniidae). Journal of Arachnology 2:1–4.

Chamberlin, J.C. 1929. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. Part I. The Heterosphyronida (Chthoniidae) (Arachnida-Chelonethida). Annals and Magazine of Natural History 10(4):50–80.

Chamberlin, J.C. 1931. The arachnid order Chelonethida. Stanford University Publications, Biological Sciences 7(1):1–284.

Dumitresco, M. & T. Orghidan. 1970. Contribution à la connaissance des Pseudoscorpions souterrains de Roumanie. Travaux de l'Institute de Spéologie "Émile Racovitza" 9:97–111.

Gertsch, W.J. 1964. A review of the genus *Hypochilus* and a description of a new species from Colorado (Araneae, Hypochilidae). American Museum Novitates 2203:1–14.

Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. Manchester University Press, Manchester, England.

Hoff, C.C. 1949. The pseudoscorpions of Illinois. Bulletin of the Illinois Natural History Survey 24:407–498.

Hoff, C.C. 1952. Some heterosphyronid pseudoscorpions from New Mexico. The Great Basin Naturalist 12:39–45.

Hoff, C.C. 1956. The heterosphyronid pseudoscorpions of New Mexico. American Museum Novitates 1772:1–13.

Hoff, C.C. 1959. The ecology and distribution of the pseudoscorpions of north-central New Mexico. University of New Mexico Publications in Biology 8:1–68.

Hoff, C.C. 1961. Pseudoscorpions from Colorado. Bulletin of the American Museum of Natural History 122:409–464.

Judson, M.L.I. 1990. Observations on the form and function of the coxal spines of some chthonioid pseudoscorpions from Cameroon (Arachnida, Chelonethida). Acta Zoologica Fennica 190:195–198.

Morikawa, K. 1960. Systematic studies of Japanese pseudoscorpions. Memoirs of the Ehime University (2B) 4:85–172.

Muchmore, W.B. 1968. A cavernicolous species of the pseudoscorpion genus *Mundochthonius* (Arachnida, Chelonethida, Chthoniidae). Transactions of the American Microscopical Society 87:110–112.

Muchmore, W.B. 1973. New and little known pseudoscorpions, mainly from caves in Mexico (Arachnida, Pseudoscorpionida). Association for Mexican Cave Studies Bulletin 5:47–62.

Muchmore, W.B. 1975. A new genus and species of chthoniid pseudoscorpion from Mexico (Pseudoscorpionida, Chthoniidae). Journal of Arachnology 3:1–4.

Muchmore, W.B. 1996. A new *Mundochthonius* from the Dominican Republic (Pseudoscorpionida: Chthoniidae). Insecta Mundi 10:104.

Parris, L.E. 1973. Caves of Colorado. Pruett Publishing, Boulder, Colorado.

Pollard, G. 1954. Fly Cave. News and notes, Colorado Grotto, National Speleological Society 3(4):1–5.

Rafalski, J. 1948. *Mundochthonius carpaticus* sp. nov., nowy gatunek zaleszczotka (Pseudoscorpionidea). [*Mundochthonius carpaticus*, a new species of Pseudoscorpionidea.] Annales Musei Zoologici Polonici 14(3):13–20. (in Polish, with English summary).

Schawaller, W. 1989. Pseudoskorpione aus der Sowjetunion, Teil 3 (Arachnida: Pseudoscorpiones). Stuttgarter Beiträge zur Naturkunde (A) 440:1–30.

Vitali-di Castri, V. 1976 [1975]. Deux nouveaux genres de Chthoniidae du Chili: *Chiliochthonius* et *Francochthonius* (Arachnida, Pseudoscorpionida). Bulletin du Muséum Nationale d'Histoire Naturelle, Paris (3) 334:1277–1291.

Vogel, B. & R.W. Ayre. 1961. New species of rare spider found in Colorado cave. NSS News 19:156.

SYNONYMY OF *CECODITHA* (CECODITHINAE) WITH *AUSTROCHTHONIUS* (CHTHONIINAE) (CHELONETHI, CHTHONIIDAE)

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ABSTRACT. The holotype of *Cecoditha parva* Mello-Leitão 1939, from Chubut Province, Argentina, is redescribed and shown to be a typical member of the genus *Austrochthonius* Chamberlin 1929. The monotypic genus *Cecoditha* Mello-Leitão 1939 is therefore a junior subjective synonym of *Austrochthonius*, while the subfamily Cecodithinae Chamberlin & Chamberlin 1945 (Tridenchthoniidae) is a junior subjective synonym of Chthoniinae Daday 1888 (Chthoniidae).

RESUMEN. El holotipo de *Cecoditha parva* Mello-Leitão 1939, de la provincia de Chubut, Argentina, es redescrito y se demuestra que es un miembro típico del género *Austrochthonius* Chamberlin 1929. El género monotípico *Cecoditha* Mello-Leitão 1939 es por lo tanto un sinónimo subjetivo posterior de *Austrochthonius*, mientras que la subfamilia Cecodithinae Chamberlin & Chamberlin 1945 (Tridenchthoniidae) es un sinónimo subjetivo posterior de Chthoniinae Daday 1888 (Chthoniidae).

Keywords: Pseudoscorpion, taxonomy, Argentina

In 1939, Mello-Leitão described a seemingly unusual new genus and species of falsescorpion, *Cecoditha parva* Mello-Leitão, from southern Argentina. Mello-Leitão assigned *Cecoditha* to the subfamily Dithinae Chamberlin (now Tridenchthoniidae Balzan), but he did not give his reasons for doing so or discuss its relationships with other genera.

Impressed by the incongruity of its characters, Chamberlin & Chamberlin (1945: 14) created a new subfamily, Cecodithinae, for *C. parva*, writing "This species, if correctly described, is unique in possessing a simple galea ("Galea sencilla") in the adult stage. This feature, together with the fact that the species also reportedly lacks coxal spines and had the tactile setae *IB* and *ISB* placed sub-medially instead of sub-basally on the dorsum of the hand of the chela, sets the species widely apart from all other known Tridenchthoniidae and necessitates its segregation in a separate subfamily." It is curious that Chamberlin & Chamberlin did not question the assignment of *C. parva* to the Tridenchthoniidae, despite their doubts about the accuracy of the original description. They might have been more cautious had they known that Mello-Leitão was capable of prodigious errors of classification (e.g., see Krantz & Platnick 1995).

With the lack of subsequent records of Cecodithinae, the systematic position of *C. parva* became increasingly doubtful. In the hope of resolving the matter, I asked to borrow the unique type of this species from the Museo de La Plata in 1982, but was informed at that time that it could not be found. Fortunately, the specimen was rediscovered in the collection years later by Lic. R.F. Arrozpide, who kindly sent it for study. Although the holotype is in poor condition, it is clearly a member of the chthoniid genus *Austrochthonius* Chamberlin.

Family Chthoniidae Daday
Subfamily Chthoniinae Daday

Chthoniinae Daday 1888: 133.
Cecodithiinae [*lapsus* for Cecodithinae] Chamberlin & Chamberlin 1945: 65; Harvey 1991: 217. NEW SYNONYMY.
Cecodithinae Chamberlin & Chamberlin – Harvey 1992: 1401.

Austrochthonius Chamberlin

Austrochthonius Chamberlin 1929: 68 (type species *Chthonius chilensis* Chamberlin 1923, by original designation); Beier 1932: 38; Vitali-di Castri 1968: 144–145; Harvey 1991: 139.
Paraustrochthonius Beier 1931: 52 (type species *Paraustrochthonius tullgreni* Beier 1931, by original designation); Beier 1932: 40; Vitali-di Castri
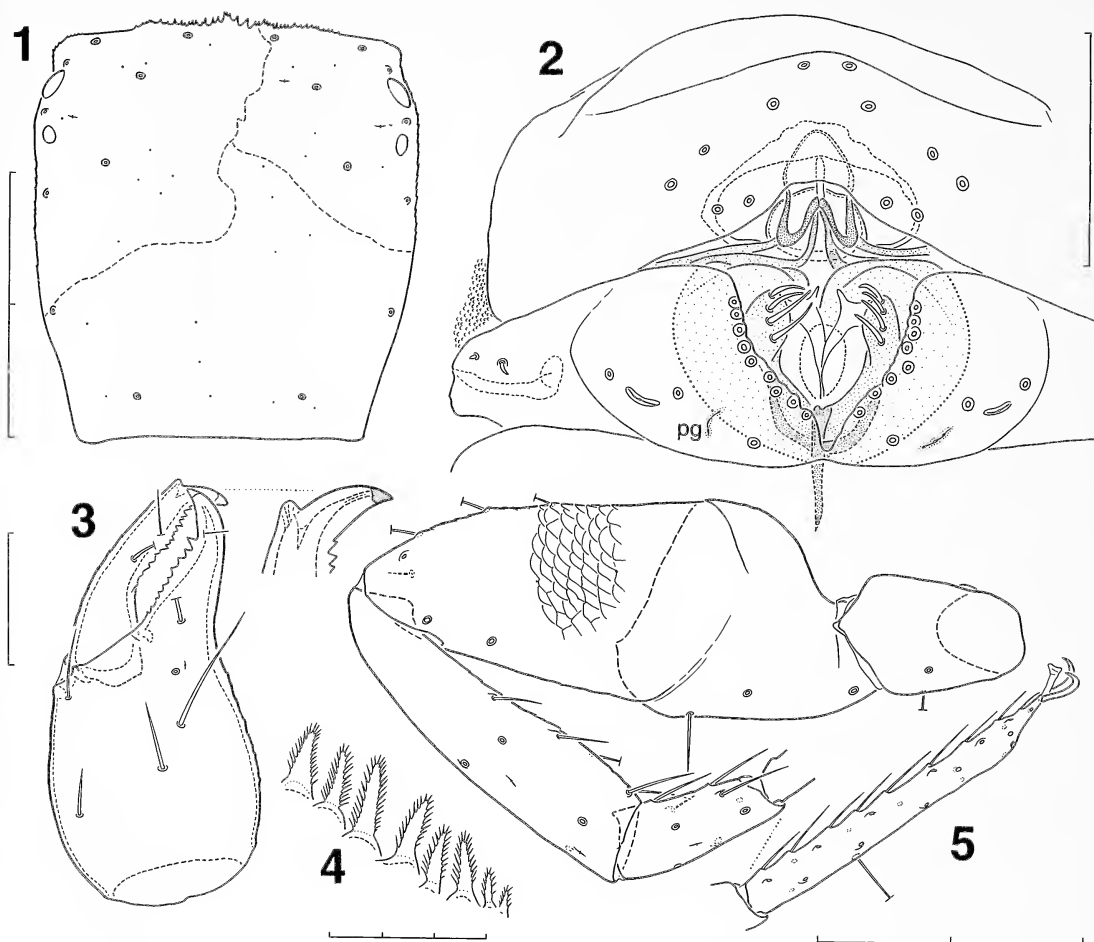
Figures 1–5.—*Austrochthonius parvus* (Mello-Leitão), holotype male. 1. Carapace (reconstructed; dots represent gland pores); 2. Genital region; 3. Left chelicera, with detail showing spinneret; 4. Coxal spines of right coxa II; 5. Right leg IV (reticulation only shown in part). Abbreviation: *pg* = pore group. Divisions of scale lines = 0.1 mm (Figs. 1–3, 5) or 0.01 mm (Fig. 4).

1968: 144–145. Synonymized by Beier 1976: 203.

Cecoditha Mello-Leitão 1939: 115–116 (type species *Cecoditha parva* Mello-Leitão 1939, by original designation); Chamberlin & Chamberlin 1945: 65–66; Harvey 1991: 218; Kury & Nogueira 1999: 13. NEW SYNONYMY.

Austrochthonius parvus (Mello-Leitão)
NEW COMBINATION
Figs. 1–9

Cecoditha parva Mello-Leitão 1939: 116–117, figs. 1a, b; Chamberlin & Chamberlin 1945: 66–67, fig. 17; Harvey 1991: 218; Kury & Nogueira 1999: 13.

Material examined.—Holotype ♂, "*Cecoditha parva* M.L./Mel.-Leit. det.; [Puerto] Madryn, Chu-

but, 18.II.1938, [M.] Bir[abén]" (Museo de La Plata, Universidad Nacional de La Plata). Specimen in poor condition—carapace broken into three pieces; right chelicera, both legs I (including coxae) and left leg IV lost—and strongly darkened as a result of storage in corked tube.

Diagnosis.—Moderately large species (e.g., movable chela finger length 0.43 mm), male with well developed spinneret tubercle, tergites I-IV with 4 setae, chelal teeth contiguous.

Description.—Carapace (Fig. 1) with weak reticulation, laterally hispid (especially anteriorly); anterior margin strongly serrate medially, but without a pronounced epistome; anterior eyes with strong lens, roughly one ocular diameter from anterior margin, poste-
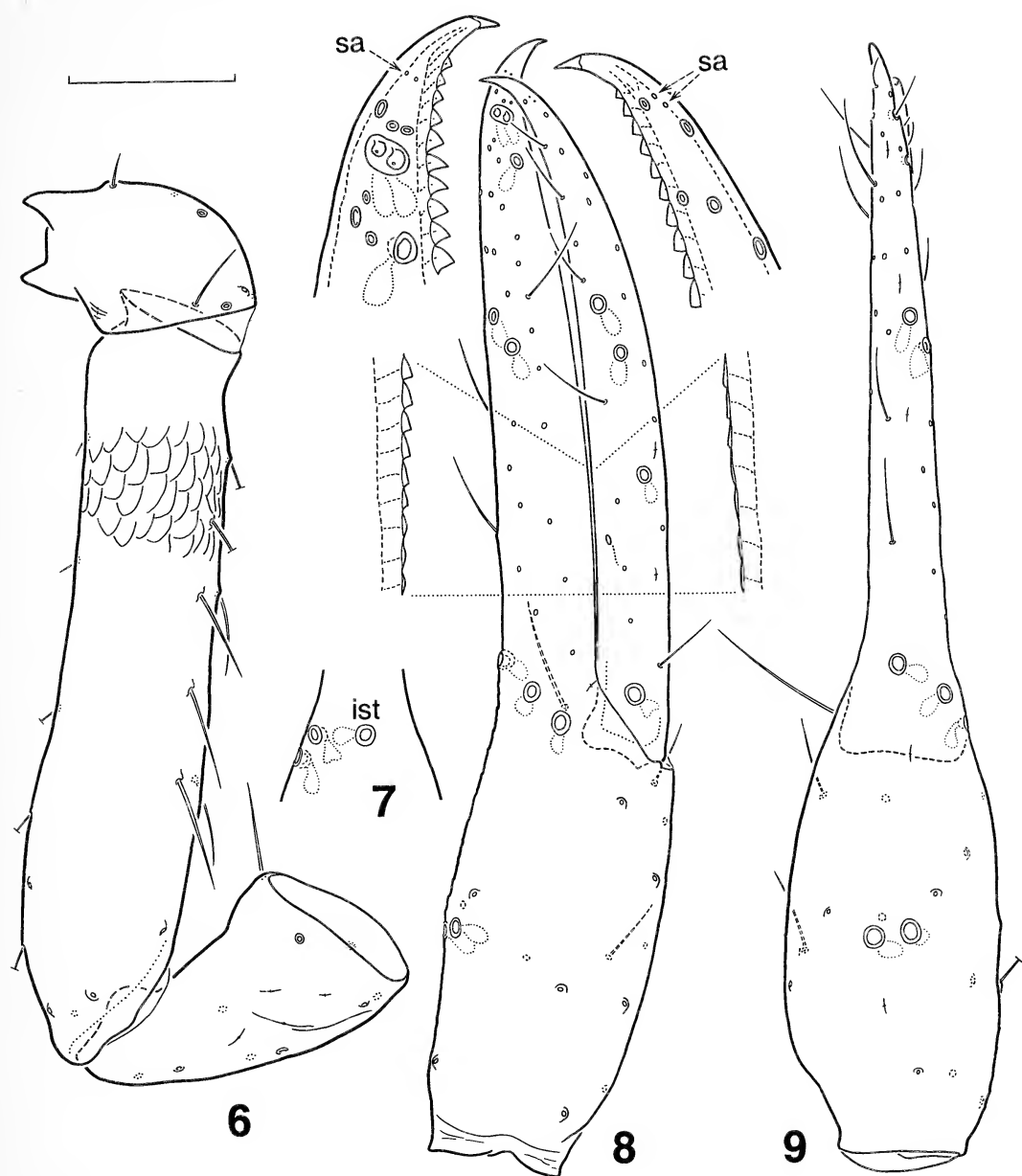
Figures 6–9.—*Austrochthonius parvus* (Mello-Leitão), holotype male, palps. 6. Trochanter, femur and patella of right palp (reticulation only shown in part). 7. Base of fixed finger of left chela, showing position of *ist*; 8. Right chela, lateral, with details of dentition and sensilla; 9. Right chela, dorsal. Abbreviation: *sa* apical sensilla. Scale line = 0.1 mm (0.05 mm for details).

rior eyes reduced to weak spots; setae 6:4:4: 2:2 (18); scattered pores present. Tergites reticulate, setae 4:4:4:4:6:6:6:6:6:4:1T2T1:0; each tergite with a row of pores just in front of setal row. Coxal setae P 5 (2 on manducatory process, subapical long):I ?:II 4:III 5: IV 5; coxa II with 7–8 bipinnate spines, bases

almost contiguous (Fig. 4); intercoxal tubercle absent. Anterior genital operculum (Fig. 2) with 12 setae; posterior operculum (Fig. 2) with (3m)6(3m), plus 8–9 setae on each side of notch (total (3m)17(3m)); remaining sternites 11:10:8:8:8:8:7:0:2, sternite X with a small, unpaired, median seta; anterior genital

sternite with three pores grouped on each side (*pg*, Fig. 2), other sternites with a normal row of pores in front of setal row; stigmata normal, not situated on a separate sclerite; pleural membrane papillate. Genitalia (Fig. 2) typical, with 4 pairs of glandular setae, *ace* elongate (see Vitali-di Castri 1976). Lateral and median genital sacs not seen. Chelicera (Fig. 3) with hand and base of movable finger scaly-reticulate; hand with 6 setae; fixed finger with 10 teeth, moveable finger with 13; flagellum of 11 blades, basal blade short; serrula exterior and serrula interior with about 13 blades; spinneret in the form of a distinct tubercle. Palp (Figs. 6–9) with femoral setae 3:5:1:2:5:1; patella with ten setae; hand with 3 proximal, 7 medial and 4 distal setae; fixed finger with a single strong seta at base; dorsum of hand moderately hispid distad of *ib/isb* and slightly depressed behind; fixed finger with 47, movable finger with 37 contiguous teeth, those of movable finger generally weaker than those of fixed finger, becoming obsolete proximally; apical sensilla (Fig. 8: *sa*) small and close together, near tip; proximal sensilla near dental margin, about ⅔ way from *b* to *sb*; trichobothria as illustrated, position of *ist* variable (compare Figs. 7 and 9). Leg IV (Fig. 5) with scaly reticulation on all segments; setae (trochanter to basitarsus) 2:3:7:9:9, basitarsal TS 0.31, telotarsal TS 0.30. Measurements (in mm; ratios in parentheses): carapace (estimated) 0.43 × 0.39; palp femur 0.45 × 0.10 (4.5), tibia 0.20 × 0.11 (1.9), hand 0.26 × 0.13 (2.0), chela 0.67 (5.3), movable finger 0.43 (finger/hand 1.7); leg IV femur 0.20 × 0.17 (1.2), patella 0.26 × 0.15 (1.7), femur+patella 0.40 (2.4), tibia 0.30 × 0.07 (4.2), basitarsus 0.14 × 0.055 (2.5), telotarsus 0.27 × 0.03 (8.6).

Remarks.—Although there was no registration number or indication of type status with the specimen, the locality details and the identification leave no doubt that this is the holotype. Kury & Nogueira's (1999) assumption that "syntypes" existed is an error, since Mello-Leitão (1939) only mentioned the male "Tipo." The original description contains many errors, the most important of which are the statements that *A. parvus* lacks eyes and coxal spines, and has only six blades in the flagellum. The measurements of the palp are also slightly lower than those given here.

This species can be separated from the oth-er members of *Austrochthonius* by the combination of characters given in the diagnosis; the well developed spinneret tubercle of the male is particularly distinctive. The presence of six setae on the hand of the single remaining chelicera is also unusual, but more material is required to determine whether this is anomalous. Vitali-di Castri (1968) found six setae on one chelicera of *A. insularis* Vitali-di Castri, the normal number being five.

ACKNOWLEDGMENTS

LITERATURE CITED

Beier, M. 1931. Zur Kenntnis der Chthoniiden (Pseudoskorpione). Zoologischer Anzeiger 93: 49–56.

Beier, M. 1932. Pseudoscorpionidea I. Subord. Chthoniinea et Neobisiinea. Das Tierreich 57:1–258.

Beier, M. 1976. The pseudoscorpions of New Zealand, Norfolk and Lord Howe. New Zealand Journal of Zoology 3:199–246.

Chamberlin, J.C. 1929. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. – Part 1. The Heterosphyronida (Chthoniidae) (Arachnida - Chelonethida). Annals and Magazine of Natural History (10) 4:50–80.

Chamberlin, J.C. & R.V. Chamberlin. 1945. The genera and species of the Tridenchthoniidae (Dithidae), a family of the arachnid order Chelonethida. Bulletin of the University of Utah 35 (23) (Biol. Ser. 9 (2)):1–67.

Daday, E. 1888. A Magyar Nemzeti Muzeum álskorpióinak áttekintése. Természetrajzi Füzetek 11:111–136, 165–192.

Harvey, M.S. 1991. Catalogue Of The Pseudoscorpionida. 726 p. Manchester Univ. Press, Manchester.

Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invertebrate Taxonomy 6:1373–1435.

Krantz, G.W. & N.I. Platnick. 1995. On *Brucharachne*, the spider that wasn't (Arachnida, Acari,

Dermanyssoidea). American Museum Novitates 3151:1–8.

Kury, A. & A.L.C. Nogueira. 1999. Annotated check list of type specimens of Arachnida in the Museu Nacional - Rio de Janeiro. I. Scorpiones, Pseudoscorpiones and Solifugae. Publicações Avulsas do Museu Nacional, Rio de Janeiro 77: 3–19.

Mello-Leitão, C. de. 1939. Pseudoscorpiónidos de Argentina. Notas del Museo de La Plata 4 (Zool. 17):115–122.

Vitali-di Castri, V. 1968. *Austrochthonius insularis*, nouvelle espèce de pseudoscorpions de l'Archipel de Crozet (Heterosphyronida, Chthoniidae). Bulletin du Muséum National d'Histoire Naturelle, Paris (2) 40:141–148.

Vitali-di Castri, V. 1976 (1975). Deux nouveaux genres de Chthoniidae du Chili: *Chiliochthonius* et *Francochthonius* (Arachnida, Pseudoscorpionida). Bulletin du Muséum National d'Histoire Naturelle, Paris (3) 334:1277–1291.

TWO NEW SPECIES OF *HADOGENES* (SCORPIONES, ISCHNURIDAE) FROM SOUTH AFRICA, WITH A REDESCRIPTION OF *HADOGENES BICOLOR* AND A DISCUSSION ON THE PHYLOGENETIC POSITION OF *HADOGENES*

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ABSTRACT. The taxonomic status of the endemic South African flat rock scorpion, *Hadogenes bicolor* Purcell 1899, is reassessed, based on a study of the types and a large series of newly-collected specimens. Specimens identified as *H. bicolor* by previous authors can be separated into at least three species on the basis of morphology, each of which occupies a discrete, allopatric distributional range. In light of this new evidence, *H. bicolor* is redescribed and two new species, *Hadogenes longimanus* and *Hadogenes newlandsi*, are described. A key is provided for the identification of the three allopatric species, and their ecology and conservation status are discussed. The phylogenetic position of *Hadogenes* is discussed in light of a recent cladistic analysis, and the monotypic family Hadogenidae Lourenço 2000 is synonymized with the family Ischnuridae Simon 1879.

Keywords: Scorpiones, Ischnuridae, *Hadogenes*

Scorpions of the genus *Hadogenes* Kraepelin 1894, commonly known as flat rock scorpions, are endemic to the Afrotropical region, where they are distributed from South Africa to Tanzania. Comprising 15 species, *Hadogenes* is the second most speciose genus in the family Ischnuridae Simon 1879, after *Opisthacanthus* Peters 1861.

With few exceptions, the distributional ranges of *Hadogenes* species are allopatric or parapatric (Newlands 1980; Prendini 1995), a tendency that appears to be related to the stenotopic ecological requirements of these scorpions. All of the currently recognized species are obligately lithophilous, inhabiting the narrow cracks, crevices and exfoliations of weathered rock outcrops. Ecomorphological adaptations that facilitate existence in this specialized habitat include extreme dorsoventral compression, elongation of the metasoma and pedipalps, greatly enlarged lateral ocelli relative to the median ocelli, presumably to aid in anterior light perception, and well-developed superciliary carinae to protect the median ocelli from abrasion (Newlands 1972a, b, 1978; Newlands & Prendini 1997). Species of *Hadogenes* are also characterized by stout, spiniform setae on the ventral surfaces of the

telotarsi and highly-curved telotarsal ungues, to provide a vice-like grip on rock surfaces. Such adaptations facilitate locomotion on rock but hinder locomotion across alternative substrata. Accordingly, these scorpions are restricted to regions of rugged, mountainous topography and readily subject to allopatric speciation when mountain ranges become separated through erosion.

As part of an ongoing revision of the taxonomy of *Hadogenes*, the status of the endemic South African flat rock scorpion, *Hadogenes bicolor* Purcell 1899, was reassessed. Purcell (1899: 437, 438) based his original description of *H. bicolor* on an adult female from "twenty miles east of Pietersburg," although his syntype series contained "several adult and young specimens." The description made no mention of the characters of the adult male *H. bicolor*. Hewitt (1918: 160, 161) subsequently described an adult male *Hadogenes* from Doornkop, near Belfast, *ca.* 200 km south of the type locality, noting "I think [the male] is referable to the same species [*H. bicolor*]." In his description of the male, Hewitt (1918) observed that the metasoma was unusually short for an adult male *Hadogenes* and that the lobe at the base of the movable finger

of the pedipalp was "larger, deeper and more acute" than in other species of the genus. Hewitt (1918) also listed two adult females from Woodbush (Pietersburg district), and described a "half-grown" male, in which the sides of the telson vesicle were finely granulated, from the same locality. The evidence supporting Hewitt's (1918) suggestion that the specimens from Woodbush and Doornkop were conspecific with each other, and with the syntypes of *H. bicolor*, was inconclusive. Nonetheless, this opinion was adopted by subsequent authors (Lawrence 1955; Lamoral & Reynders 1975).

Hadogenes bicolor was not reviewed until Newlands (1980) redescribed the species on the basis of newly-collected material (an adult male from Leopard's Crag and an adult female from Haffenden Heights), and again noted the large basal lobe of the movable finger and the short metasoma of the adult male as diagnostic characters. It is unclear whether Newlands (1980) actually examined the syntypes, for he listed the type specimens as "Female holotype and several nymphs housed in the Transvaal Museum (TMSA 4062) from 32 km east of Pietersburg." During the present investigation, the syntype series, deposited in the South African Museum, was found to comprise an adult male, two adult females, a subadult female, a juvenile male, and a juvenile female.

Newlands' (1980) redescription of *H. bicolor* was never published. However, Newlands & Cantrell (1985) published electrophoretic and cytogenetic data collected by Newlands (1980), as well as Newlands' (1980) key to the species of *Hadogenes*, in which the short metasoma of the adult male was yet again provided as a diagnostic character for *H. bicolor*. Following Newlands (1980), Newlands & Cantrell (1985) pointed out that the electrophoretic banding patterns of venom proteins from specimens of *H. bicolor* collected at two localities, *viz.* Haffenden Heights (Letaba district, Northern Province) and Zusterstroom (Bronkhorstspruit district, Gauteng Province), were distinctly different. Specimens from Zusterstroom displayed a protein component that was absent in specimens from Haffenden Heights, *ca.* 180 km northeast. Newlands & Cantrell (1985: 42) suggested that these differences might be indicative of a cryptic species complex (Paterson 1991), as "no morphological differences
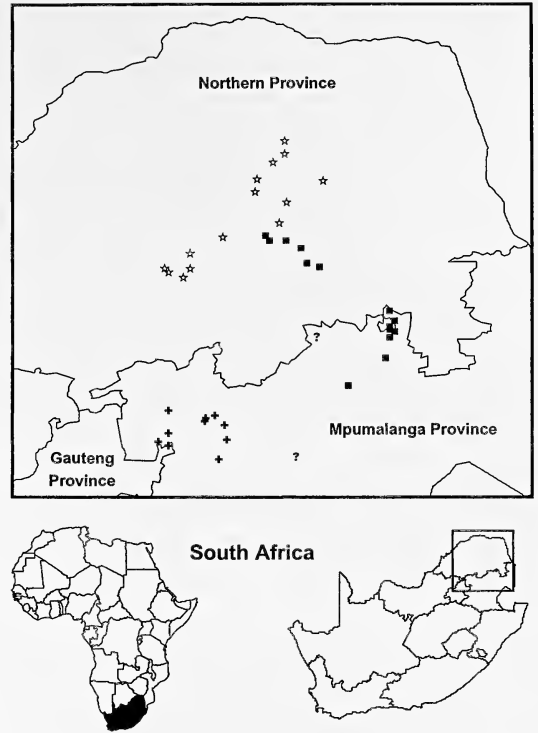
Figure 1.—Map showing the distribution of *Hadogenes bicolor* Purcell 1899 (■), *Hadogenes longimanus* new species (+), and *Hadogenes newlandsi* new species (★) in South Africa. The specimens from Doornkop and Steelpoort (?) have been provisionally identified as *H. longimanus*, but may comprise another undescribed species in this complex.

... could be detected" between specimens from the two localities.

In the present study, specimens from across the distributional range of *H. bicolor*, including the material examined by Hewitt and Newlands, and newly collected material, were compared with the syntypes. Since *Hadogenes* species are notoriously difficult to identify without examination of the adult male, new series of *H. bicolor*, including adults of both sexes, were collected from several localities in the same and neighboring districts as the type locality, and in the districts from which the other material, examined by Hewitt and Newlands, originated. Some of these localities are as much as 100 km north to 200 km south of the type locality of *H. bicolor*.

Examination of this new material has confirmed the suggestion of Newlands (1980) and Newlands & Cantrell (1985) that more than

Table 1.—The currently accepted species of *Hadogenes* Kraepelin 1894 (Scorpiones, Ischnuridae), with countries of distribution compiled from Prendini (1995). [1] Species of dubious validity. [2] Species complexes.

Hadogenes angolensis Lourenço 1999[1]	Angola
Hadogenes bicolor Purcell 1899	South Africa
Hadogenes gracilis Hewitt 1909	South Africa
Hadogenes granulatus Purcell 1901	Botswana, Mozambique, Zambia, Zimbabwe
Hadogenes gunningi Purcell 1899	South Africa
Hadogenes lawrencei Newlands 1972	Namibia
Hadogenes longimanus new species	South Africa
Hadogenes minor Purcell 1899	South Africa
Hadogenes newlandsi new species	South Africa
Hadogenes paucidens Pocock 1896[1]	Democratic Republic of Congo, ?Tanzania
Hadogenes phyllodes Thorell 1877[2]	Namibia, South Africa
Hadogenes taeniurus (Thorell 1877)	Angola, Namibia
Hadogenes tityrus (Simon 1888)[2]	Namibia, South Africa
Hadogenes trichiurus (Gervais 1843)[2]	South Africa
Hadogenes troglodytes (Peters 1861)	Botswana, Mozambique, South Africa, Zimbabwe
Hadogenes zuluanus Lawrence 1937	South Africa, Swaziland
Hadogenes zumpti Newlands & Cantrell 1985	?Namibia, South Africa

one species is involved. However, contrary to the view expressed by these authors, several consistent morphological differences could be identified between specimens from the localities at which samples, analyzed electrophoretically by Newlands (1980) and Newlands & Cantrell (1985), were found to differ in venom protein composition.

Specimens identified as *H. bicolor* by previous authors can be separated into at least three species on the basis of morphology, each of which occupies a discrete, allopatric distributional range (Fig. 1). In light of this new evidence, *H. bicolor* is redescribed and two new species, *Hadogenes longimanus* and *Hadogenes newlandsi*, are described. As in other closely related species of *Hadogenes*, adult female specimens of all three species are superficially similar morphologically, whereas adult male specimens differ markedly. However, adult females of all three species can also be reliably identified on the basis of several consistent diagnostic characters. These characters are summarized in a key to the identification of the three species. Recognition of the two new species raises the number of currently accepted species of *Hadogenes* to 17 (Table 1).

Lourenço's (1999, 2000) recent proposals to transfer *Hadogenes* to the Scorpionidae Latreille 1802, or provide a monotypic family Hadogenidae Lourenço 2000 are unsupported by cladistic analysis (Prendini 2000). This contribution concludes with a discussion of the phylogenetic position of *Hadogenes*, in which the Hadogenidae is synonymized with the Ischnuridae.

METHODS

Material examined, including the type specimens of *H. bicolor*, *H. longimanus* and *H. newlandsi*, is deposited in the following collections: South African Museum, Cape Town (SAMC); Transvaal Museum, Pretoria, South Africa (TMSA); Albany Museum, Grahamstown, South Africa (AMGS); Natal Museum, Pietermaritzburg, South Africa (NMSA); American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CASC). Tissue samples of the three species, stored in absolute ethanol at −20 °C, have been retained separately for DNA isolation and sequencing in the Ambrose Monell Collection for Molecular and Microbial Research at the American Museum of Natural History, New York (AMC).

Illustrations of *H. bicolor*, *H. longimanus* and *H. newlandsi* were produced using a Wild stereomicroscope and camera lucida. Measurements were made with Mitutoyo® digital calipers. Color designation follows Smithe (1974, 1975, 1981), trichobothrial notation follows Vachon (1974), and mensuration follows Stahnke (1970) and Lamoral (1979). Morphological terminology follows Couzijn

(1976) for the segmentation of legs, Hjelle (1990) and Sissom (1990) for the segmentation of pedipalps, and Stahnke (1970), Lamoral (1979), Newlands (1980), Sissom (1990) and Newlands & Prendini (1997) for remaining features.

Key to the identification of *Hadogenes bicolor* Purcell 1899, ***Hadogenes longimanus*** new species and ***Hadogenes newlandsi*** new species

1. Pedipalp chela with 5–8 trichobothria in the *i* series (Fig. 21) . . . .*Hadogenes longimanus*
   Pedipalp chela with two trichobothria in the *i* series (Figs. 10, 32). 2
2. Pedipalp chela of adult ♂ and ♀ with a pronounced lobe, distal to the notch in the fixed finger (Figs. 8, 9); metasoma of adult ♂ length *ca.* 55% of total length (Figs. 2, 3), with telson smooth and lateral surfaces of metasomal segment V sparsely granular (Fig. 33) . . . .*Hadogenes bicolor*
   Pedipalp chela of adult ♂ and ♀ without a pronounced lobe, distal to the notch in the fixed finger (Figs. 26, 30); metasoma of adult ♂ length *ca.* 60% of total length (Figs. 22, 23), with telson and lateral surfaces of metasomal segment V densely granular (Fig. 35). . . . .*Hadogenes newlandsi*

Hadogenes bicolor Purcell 1899
Figs. 1–10, 33, 36, Table 2

Hadogenes bicolor Purcell 1899: 437, 438.
Hadogenes bicolor: Lawrence 1955: 251 (part); Lamoral & Reynders 1975: 538 (part); Newlands 1980 (unpublished): 99–105 (part), figs. 48 (part), 49–53; Newlands & Cantrell 1985: 40, 42, 44 (part); Kovařík 1998: 132; Fet 2000: 387.

Types.—SOUTH AFRICA: *Northern Province:* Pietersburg district: Syntypes: ♂, 2♀, subadult ♀, juv ♂, juv ♀ (SAMC 4062), 20 miles east of Pietersburg [23°54′S, 29°47′E]. The ♂ is hereby designated as the lectotype of *H. bicolor* and the remaining specimens as paralectotypes.

Diagnosis.—Hadogenes bicolor* is the sister species of *H. longimanus*. These two species are both characterized by a pronounced lobe, distal to the notch in the fixed finger of the pedipalp chela of adult ♂ and ♀, and a relatively short metasoma in the adult ♂, compared with *H. newlandsi* and other *Hadogenes* species. Accordingly, these characters are hypothesized to be synapomorphic for *H. bicolor* and *H. longimanus*.

Hadogenes bicolor can be separated from *H. longimanus* by the presence of two, rather than 5–8, trichobothria on the internal surface of the pedipalp chela. *Hadogenes bicolor* can be further distinguished from *H. newlandsi* by the smooth telson of the adult ♂, and the longer pedipalp segments of adult ♂ and ♀.

Description.—The following description is based on the lectotype ♂ (SAMC 4062), a paralectotype ♀ (SAMC 4062), the ♂ from Leopard's Crag (TMSA 18004) and ♀ from Haffenden Heights (TMSA 18005) described by Newlands (1980), and a newly collected ♂

(Figs. 2, 3) and ♀ (Figs. 4, 5) from Jongmansspruit (SAMC C4585). It is intended to complement Purcell's (1899) original description and Newlands' (1980) unpublished redescription.

Color: (SAMC C4585). Pale chelicerae, legs, and telson contrasting markedly with darker carapace, pedipalps, tergites and metasomal segments I-V. Sternites also paler than tergites and metasomal segments. Pedipalps, Buff 24 on chela manus and intercarinal surfaces of patella and femur, Sepia 119 on carinae and chela fingers; cheliceral manus, legs (except prolateral surfaces of femora), telson, sternites, pectines, and genital operculum, Straw Yellow 36; cheliceral fingers, carapace, tergites (♂) and prolateral surfaces of leg femora, Sepia 119; tergites (♀) and metasomal segments I-V, Dark Brownish-olive 129.

Carapace: Three pairs of lateral ocelli, equal in size to median ocelli (Fig. 6). Median ocular tubercle with superciliary carinae well developed, protruding above ocelli, and interocular sulcus distinct. Anterior margin of carapace with median notch well developed, such that triangular inset is situated far back and frontal lobes protrude anteriorly. Anteromedian sulcus deep, suturiform, furcating anteriorly around triangular inset. Median longitudinal suture distinct, continuous from anterior furcated sutures, through ocular tubercle to posterior furcated sutures, which converge on ocular tubercle from posterior carapace margin. Posterior furcated sutures obsolete, discontinuous. Posteromedian and posteromarginal sulci distinct, but shallow. Paired median lateral and posterolateral sulci also distinct, shallow. Carapace entirely gran-
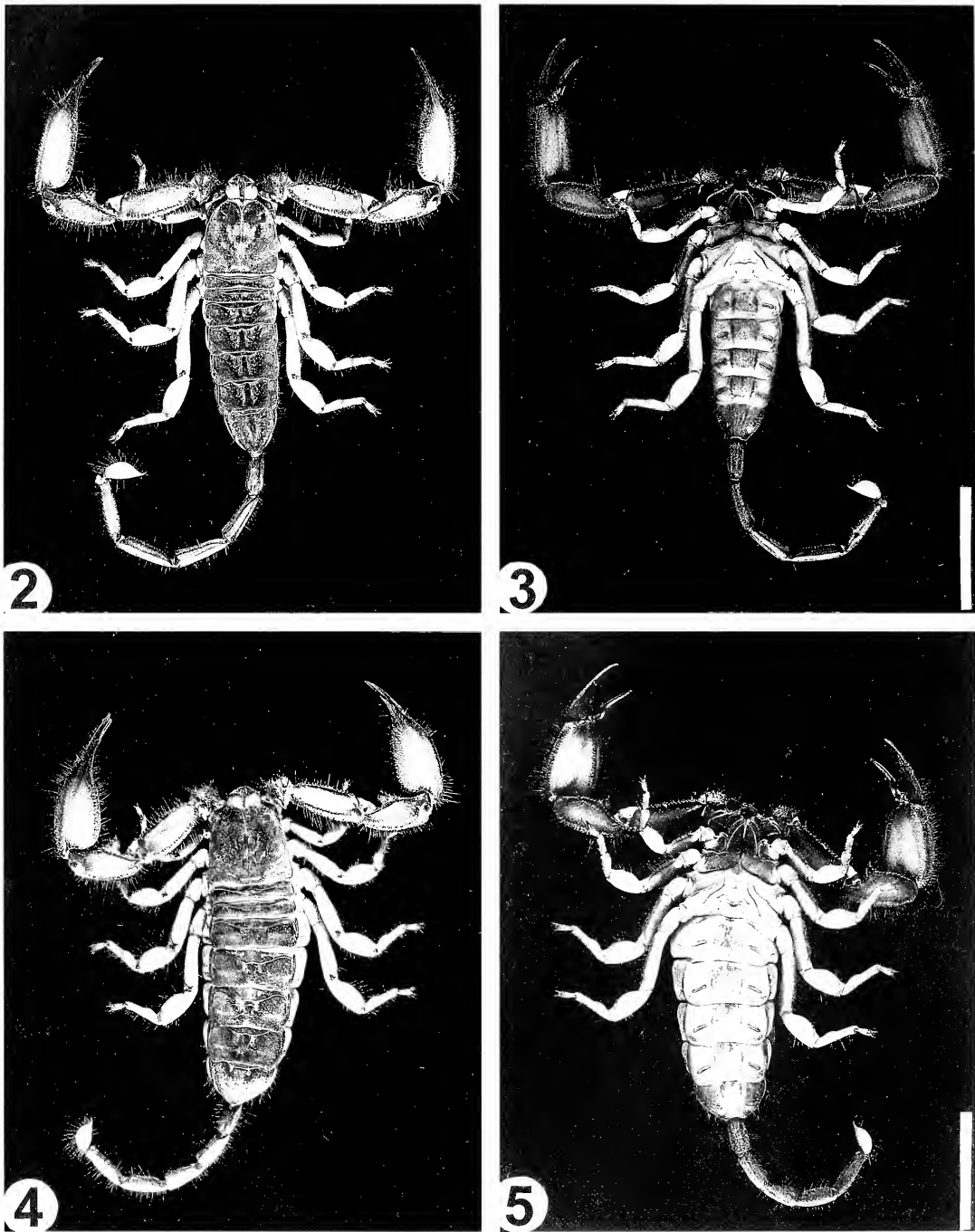
Figures 2–5.—*Hadogenes bicolor* Purcell 1899, habitus of ♂ and ♀ (SAMC C4585). 2. Dorsal aspect, ♂; 3. Ventral aspect, ♂; 4. Dorsal aspect, ♀; 5. Ventral aspect, ♀. Scale bars = 20 mm.

ular, except for surfaces of frontal lobes, median lateral, posterolateral and posteromarginal sulci, which are smooth. Granulation almost uniformly fine, becoming coarse on antero-ocular and anterolateral surfaces.

Chelicerae: Movable finger with distal internal tooth slightly smaller than distal external tooth, and apposable. Ventral aspect of fingers and manus with long, dense macrosetae.

Pedipalps: Femur pentacarinate, with four

6

7

Figures 6–7.—*Hadogenes bicolor* Purcell 1899, carapace and sternite VII of ♀ (SAMC C4585), showing carinae, depressions and sulci. 6. Carapace; 7. Sternite VII. Scale bar = 4 mm.

distinct carinae; ventroexternal carina obsolete, reduced to a few granules proximally; dorsoexternal and externomedian carinae granular, dorsointernal and ventrointernal carinae costate-granular, composed of very large heavily sclerotized granules; dorsoexternal and ventral intercarinal surfaces finely and uniformly granular; internal intercarinal surfaces smooth, except for a few scattered spiniform granules. Femur length 63% (62–64%) greater than width in ♂, 60.5% (58–63%) greater in ♀ (Table 2).

Patella with seven carinae, six of which are distinct, whereas the dorsoexternal carina is obsolete; dorsointernal and ventrointernal carinae costate to costate-granular; internomedian carina costate-granular, composed of

very large heavily sclerotized spiniform granules; externomedian and ventroexternal carinae granular; dorsoexternal and ventral intercarinal surfaces finely and uniformly granular, becoming granulo-reticulate on ventral surfaces; internal intercarinal surfaces smooth; anterior process strongly developed. Patella length 45% (44–46%) greater than width in ♂, 41% (40–42%) greater in ♀.

Chela pentacarinate, with three distinct carinae; dorsal secondary and digital carinae obsolete (Figs. 8, 9); external secondary carina strongly developed, costate to costate-granular; ventroexternal carina strongly developed, crenulate, aligned parallel to longitudinal axis of chela, with distal edge disconnected from external movable finger condyle and directed toward a point between external and internal movable finger condyles, but closer to external condyle (Fig. 10); ventromedian carina obsolete, reduced to a vestigial granule proximally; ventrointernal carina also obsolete; internomedian and dorsointernal carinae weakly developed, each comprising a series of isolated spiniform granules; dorsomedian carina strongly developed, composed of a continous double row of spiniform granules; dorsal and ventrointernal intercarinal surfaces smooth, reticulate; dorsointernal intercarinal surfaces with scattered spiniform granules, becoming finely granular on internal surface of fixed finger; external intercarinal surfaces coarsely granular. Chela with a pronounced, conical lobe on movable finger and corresponding notch in fixed finger; fixed finger additionally with a pronounced, conical lobe distal to the notch, and a smaller, rounded lobe proximally. Dentate margins of chela fingers with double row of denticles, which are fused at the lobe/notch. Chela length along ventroexternal carina 46.5% (44–49%) greater than chela width in ♂, and 36.5% (33–40%) greater in ♀; chela width 50.5% (44–57%) greater than chela height in ♂, and 52% (49–55%) greater in ♀; length of movable finger 9% (5–13%) less than length along ventroexternal carina in ♂, and 4% (1–7%) less in ♀.

Trichobothria: Neobothriotaxic major, type C (Figs. 8, 10), with the following segment totals (Table 2): femur 3 (1 d; 1 i; 1 e), patella 68–96 (2 d; 1 i; 27–34 v; 38–59 e) and chela 77–92 (67–82 manus; 10 fixed finger, including 2 i). Total number of τ per pedipalp, 148–191. Only femoral τ, τ in the d and i series of
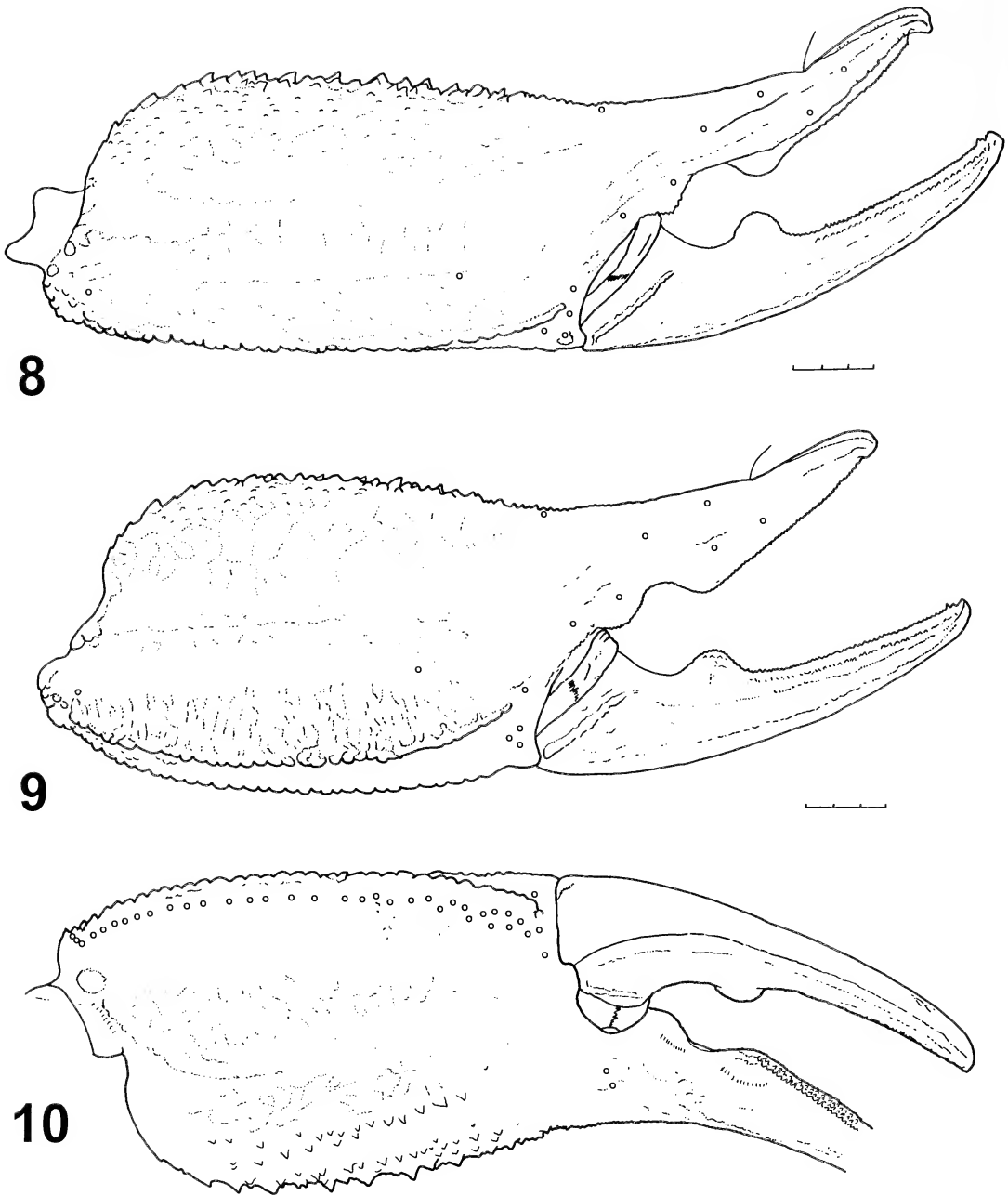
Figures 8–10.—*Hadogenes bicolor* Purcell 1899, dextral pedipalp chelae of ♂ and ♀ (SAMC C4585), showing trichobothrial distribution and shape of lobes on fixed and movable fingers. 8. Dorsal aspect, ♂; 9. Dorsal aspect, ♀; 10. Ventrointernal aspect, ♀. Scale bars = 3 mm.

the patella, and τ in the D, d, e and i series of the chela are stable in number and distribution. External and ventral τ of the chela and patella are numerically and distributionally too variable for diagnostic purposes.

Mesosoma: Tergites each with paired sub-median depressions and obsolete median carina. Pre-tergites of ♂ and ♀ smooth and shiny. Post-tergites of ♂ covered with very fine and even granulation, imparting a matte appearance to all surfaces, except median carina and submedian depressions, which are

smooth; post-tergites of ♀ smooth and shiny. Sternites smooth and shiny, each with paired longitudinal depressions internal to spiracles. Sternite VII additionally with a pair of shallow posterolateral oval depressions (more prominent in ♂) and a pair of obsolete carinae, converging distally towards a shallow notch in distal apex (Fig. 7). Sternite VII 16.5% (9–24%) wider than long in ♂, 26% (19–33%) wider than long in ♀ (Table 2).

Pectines: ♂ with mesial margin of first proximal median lamella of each pecten angular, pectinal teeth present along entire posterior margin; ♀ with mesial margin of first proximal median lamella shallowly curved, proximal fifth of posterior margin devoid of teeth. Pectinal teeth: 19–20/18–20 (♂), 16–17/15–16 (♀).

Sternum: Subpentagonal. Median longitudinal furrow shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Suboval, completely divided longitudinally, with genital papillae present (♂). Subcordate, partially connected by a membrane in anterior two-thirds, with distinct distal lobes in posterior third, and with genital papillae absent (♀).

Legs: Femora each with paired granular carinae on prolateral surface. Basitarsi each with a few spiniform setae on prolateral and retrolateral margins, decreasing in number from anterior to posterior legs. Telotarsi each with two rows of three ventrosubmedian spiniform setae and a basal row of 4–6 ventromedian spinules. Telotarsal laterodistal lobes truncated; median dorsal lobes extending to ungues. Telotarsal ungues short, distinctly curved, and equal in length. Retrolateral pedal spurs absent.

Metasoma and telson: Metasomal segment I 20% (10–30%) wider than high posteriorly (Table 2). Metasomal segments I-V progressively increasing in length, and decreasing in width, with segment V 36.5% (33–40%) narrower than segment I. Metasoma slender, width percentage of length for segment I, 40% (37–43%) in ♂, 53% (50–56%) in ♀; for II, 23.5% (23–24%) in ♂, 31.5% (31–32%) in ♀; for III, 21.5% (20–21%) in ♂, 28.5% (28–29%) in ♀; for IV, 18.5% (18–19%) in ♂, 26.5% (25–28%) in ♀; and for V, 17% (16–18%) in ♂, 23.5% (23–24%) in ♀. Telson vesicle 13% (9–17%) wider than metasomal segment V in ♂, 5% (2–8%) wider in ♀; oval in shape, with flattened dorsal surface and rounded ventral surface (Fig. 33), height 36% (33–39%) of length. Aculeus short, 23% (21–25%) of vesicle length, and sharply curved. Total length of metasoma 17.5% (16–19%) longer than combined length of prosoma and mesosoma in ♂, but 14.5% (10–19%) shorter in ♀.

Eight carinae on segment I, six carinae on segments II-IV, and five carinae on segment V. Dorsosubmedian carinae of segment I becoming obsolete distally, but distinct throughout length of segments II-V. Median lateral carinae fully developed on segment I, but absent from segments II-V. Segments I-IV with closely paired ventrosubmedian carinae, fused into a single ventromedian carina on segment V. Ventrosubmedian and ventrolateral carinae costate on segment I, costate to costate-granular on segments II-IV. Ventrolateral and ventromedian carinae of segment V composed of spiniform granules. Median lateral and dorsosubmedian carinae costate on segment I, dorsosubmedian carinae costate to costate-granular on segments II-V (♀), or costate-granular on segment II, but composed of spiniform granules on segments III-V (♂). Dorsosubmedian carinae of metasomal segments II-III each terminating distally with an enlarged, spiniform granule; dorsosubmedian carinae of other metasomal segments without spiniform granules distally. Intercarinal surfaces smooth, except for lateral surfaces of segments II-V in ♀. Telson smooth, covered in long macrosetae.

Hemispermatophore: Doubled hook near the base of the distal lamella; distal crest truncate (Fig. 36).

Geographic variation: Specimens from lower elevation in the Phalaborwa and Pilgrim's Rest districts are larger, and lighter in color (especially the chelicerae, pedipalps, legs, and telson), than typical specimens from high elevation in the Letaba and Pietersburg districts.

Ontogenetic variation: The presence of a lobe on the movable finger of the pedipalp chela and a corresponding notch in the fixed finger is indicative of sexual maturity in all species of *Hadogenes*, except ♂ and ♀ *Hadogenes zumpti* Newlands & Cantrell 1985, and ♀ of certain species in the *Hadogenes tityus* (Simon 1888) complex (Newlands & Prendini 1997). The lobe and corresponding notch are absent from the fingers of the pedipalp chela

in subadults and juveniles, developing in the final instar of species, such as *H. bicolor*, in which these characters are present in the adults.

In the specimens of *Hadogenes* examined for this study, sexual maturity was assessed by the presence of the lobe and notch in ♂ and ♀, and by the presence of fully developed paraxial organs in ♂ or the gravid condition in ♀. The elongated metasoma (longer than the combined length of prosoma and metasoma), a secondary sexual characteristic only acquired in the final instar ♂ (Lamoral 1979; Newlands 1980), is a further indication that ♂ specimens are adult. In all species of *Hadogenes*, juvenile ♂ and ♀ resemble each other, and adult ♀, very closely in general morphological features (besides the absence of the lobe and notch on the pedipalp chela finger) until the final instar. The metasoma of the juvenile ♂ is also shorter than the combined length of the prosoma and mesosoma.

Sexual dimorphism: The characters of primary external sexual dimorphism are the undivided genital operculum of the ♀, which opens in a single flap, whereas in the ♂, the operculum consists of two unconnected sclerites which open independently and cover a pair of genital papillae. Secondary sexual characters observed in adult ♂, compared with adult ♀ and juveniles of both sexes, are as follows: more pronounced lobes on the fixed and movable fingers of the pedipalp chela, and a more pronounced notch in the fixed finger; longer, more slender pedipalps; more slender mesosoma; elongated metasoma (longer than the combined length of the prosoma and mesosoma); increased granulation of the carapace, tergites and metasoma; greater number of pectinal teeth.

Chromosome number: Newlands (1980) recorded a chromosome number of $2n = 96$, based on testicular and ovarian tissue, but noted that the quadruploid number ($2n = 192$) was also common.

Remarks: The ♂ specimen from Doornkop near Belfast, described by Hewitt (1918), is provisionally considered to be conspecific with *H. longimanus*, but may represent another undescribed species in this complex, whereas the three specimens from Woodbush, mentioned by Hewitt (1918), are conspecific with *H. newlandsi*. Newlands' (1980) material examined includes specimens of *H. bicolor*, *H.*

longimanus, and *H. newlandsi*; and his map of the distributional range of *H. bicolor* plots records for all three species. Electrophoretic data presented for *H. bicolor* from Zusterstroom (Bronkhorstpruit district, Gauteng Province) by Newlands (1980) and Newlands & Cantrell (1985) are applicable to *H. longimanus*.

Distribution.—*Hadogenes bicolor* is restricted to rocky outcrops along the Drakensberg escarpment in the Mpumalanga and Northern Provinces of South Africa (Fig. 1), at an elevation between 1000–2000 m. Most of the recorded localities fall in the square bounded by 24–25°S latitude and 30–31°E longitude, and occur at an elevation above 1200 m, which is generally higher than the elevation at which *H. longimanus* and *H. newlandsi* have been recorded.

In addition to the localities recorded in the material examined, Newlands' (1980: 100) records of *H. bicolor* from Boyne (Northern Province, Thabamoopo district) and Perkoe (Northern Province, Phalaborwa district [Farm Perkeo]) are probably referable to this species. However, Newlands' (1980: 100) records of *H. bicolor* from Lillie, Zeekoegat and Shaholle (Northern Province, Phalaborwa district) may be referable instead to *Hadogenes troglodytes* (Peters 1861).

Ecology.—*Hadogenes bicolor* is an obligately lithophilous scorpion, which inhabits the narrow cracks and crevices of weathered dolerite and granite rocks, but can also be found under large flat rocks resting on bedrock. Most of the distributional range of *H. bicolor* occurs in Northeastern Mountain Grassland (Bredenkamp et al. 1996), receiving an annual of rainfall of 700–1100 mm. However, on the lower eastern slopes and foothills of the Drakensberg escarpment (Northern Province, Phalaborwa district), the species occurs in Sour Lowveld Bushveld (Van Rooyen & Bredenkamp 1996b), which receives a rainfall of 600–1000 mm annually.

This species is sympatric with *Opistophthalmus glabrifrons* Peters 1861, *Pseudolychas pegleri* (Purcell 1901) and *Uroplectes triangulifer* (Thorell 1876) in most of its range. It has also been recorded in sympatry with *Opisthacanthus validus* Thorell 1876 at Bourke's Luck, Blyde River Canyon, and with *Parabuthus transvaalicus* Purcell 1899 and *Uroplectes olivaceus* Pocock 1896 at Jong-

mansspruit. Prey remains in the crevices inhabited by these scorpions commonly included the rings of spirobolid and harpagophorid millipedes (Myriapoda).

Conservation status.—As with other species of *Hadogenes* in southern Africa, *H. bicolor* is faced with two main threats: habitat destruction and collection for the international trade in exotic pets. *Hadogenes* species are especially vulnerable to the former because they commonly occur on granitic inselbergs, which are quarried in many parts of South Africa to provide gravestones, chipstone and other materials requiring fine-grained igneous rock. This is the case with *H. newlandsi* (see below), whose habitat has been extensively quarried in the Pietersburg and Soutpansberg districts. Fortunately, species inhabiting sedimentary geology are less vulnerable to this land use, but may still be eradicated by urbanization, as with *Hadogenes gunningi* Purcell 1899, a threatened species that inhabits sandstones and quartzites in the highly urbanized Gauteng Province of South Africa (including the cities of Johannesburg and Pretoria).

Hadogenes bicolor is less vulnerable to habitat destruction through industry or urbanization than many other species of *Hadogenes* because its distributional range coincides with areas of high ecotourism potential along the scenic Drakensberg escarpment. A large proportion of the known range of *H. bicolor* is already protected within existing parks, viable populations having been recorded from the Blyde River Canyon, Pilgrim's Rest and Lekgalameetse nature reserves. However, in unprotected areas throughout the region, the species faces the additional threat of habitat destruction through afforestation, a land-use practice that is not conducted in the regions of lower rainfall occupied by species such as *H. longimanus* and *H. newlandsi*.

In addition to habitat destruction, *Hadogenes* scorpions are extremely vulnerable to overharvesting for the international pet trade. They are much sought after as exotic pets because of their large size, unusual flattened appearance, generally docile temperament and mild venom. However, their specialized ecological requirements make them poor candidates for prolonged survival under captive conditions. Whereas these scorpions may live for more than 30 yr in the wild (Newlands

1980), captive specimens seldom survive more than a few years, even when apparently healthy. Moreover, unlike other common pet scorpion species, e.g., *Pandinus imperator* (C.L. Koch 1841), *Hadogenes* are notoriously difficult to breed in captivity, with the result that wild populations are placed under continued pressure from harvesting. Wild populations are expected to be slow to repopulate after harvesting for the following reasons. Females have gestation periods of up to 18 mo and produce small broods ($\bar{x} = 20$) compared with other scorpions (Williams 1971; Newlands 1980). Young are relatively altricial, spending several months on their mother's terga before their first ecdysis and subsequent departure (Williams 1971), thereby further protracting the period before a ♀ can give birth to her next brood. Age to sexual maturity is 8–10 yr in these scorpions (Newlands & Cantrell 1985), during which period juveniles must run the gauntlet of natural predation (including cannibalism).

Presently, the most commonly imported pet trade species appears to be *H. troglodytes*, usually mistakenly sold under the name *H. bicolor* (pers. obs.). Traders have been unwilling to divulge their sources, but wild-caught specimens are suspected to have originated in Mozambique, Zimbabwe and the Northern Province of South Africa.

Material examined.—SOUTH AFRICA: *Mpumalanga Province:* Pilgrim's Rest district: ♂ (TMSA 10100), Blyde River, Lydenburg [24°38′S, 30°47′E], 14 January 1971, N.H.G. Jacobsen; juv ♂ (TMSA 12515), Blyde River Canyon Nature Reserve [24°35′S, 30°49′E], 8 May 1974, N.H.G. Jacobsen; ♀ (AMNH), 2 juv ♂, juv ♀ (AMC), Bourke's Luck Potholes, Blyde River Canyon Nature Reserve [24°40′S, 30°49′E], 12 July 2000, L. Prendini and M. MacFarlane, grassland, with mixed bushveld at edge of canyon, under sandstone; ♂ (AMGS), Dientje G.M., Vaalhoek, near Pilgrim's Rest [24°39′S, 30°47′E], Miss S. Preller; subadult ♀ (AMGS 4704), Dientje P.O., Vaalhoek [24°43′S, 30°47′E], S. Preller. *Northern Province:* Letaba district: ♀ (SAMC C1602), juv ♀ (SAMC C1613), Serala Wilderness Area, near Tzaneen, 24°00′S, 30°04′E, 30 August 1980, M. Stiller, under flat rocks on steep mountainside, grass, rocks; ♂ (TMSA 18004), 2♀ (TMSA 17449, 18005), Leopard's Crag, 50 km W of Haffenden Heights [Lekgalameetse Nature Reserve, 24°09′S, 30°13′E, I.H. Davidson; 6♀ (TMSA 17794, 17795, 17797—17800), Haffenden Heights, The Downs [Farm Haf-

fenden Heights 35, Lekgalameetse Nature Reserve], 24°07′S, 30°07′E, 26 June 1977, B.P.W. Fratscher. Pietersburg district: 2 juv ♂ (TMSA 17456, 17459), juv ♀ (TMSA 17457), 19 miles E of Pietersburg [23°54′S, 29°47′E], 26 December 1967, G. Newlands. Phalaborwa district: ♂, ♀ (SAMC C4585), Jongmansspruit, on Blyde River, near Swadini [24°30′S, 30°47′E], 3–8 January 1999, I. Engelbrecht & D. Eagan, in crevices in granite rocks; ♂, ♀, subadult ♂ (AMNH), juv ♀ (AMC), Peninsula trail, Blyderivierspoort Dam, Blyde River Canyon Nature Reserve [24°33′S, 30°48′E], 13 July 2000, L. Prendini, M. MacFarlane, and K.M.A. Prendini, mixed bushveld, crevice in quartz.

Hadogenes longimanus new species
Figs. 1, 11–21, 34, 37, Table 2

Hadogenes bicolor Purcell 1899: Hewitt 1918: 160, 161 (part), pl. 30, figs. 88, 89; Newlands 1980 (unpublished): 99–105 (part), fig. 48 (part); Newlands & Cantrell 1985: 40, 42, 44 (part).

Types.—SOUTH AFRICA: Holotype ♂ (SAMC C4602), *Mpumalanga Province:* Groblersdal district: 20 km S of Groblersdal on road to Middelburg, 25°20.30′S, 29°22.85′E, 13 January 2000, L. Prendini & I. Engelbrecht, mixed bushveld, crevices in granite rocks, 1077 m. Paratypes: *Gauteng Province:* Bronkhorstspruit district: ♂ (TMSA 17452), 2♀ (TMSA 17453, 17460), Farm Zusterstroom 447, 25°35′S, 29°01′E, 4 November 1977, G. Newlands. *Mpumalanga Province:* Bronkhorstspruit district: ♀ (SAMC C1600), Bundu Inn, Bronkhorstspruit to Groblersdal [25°29′S, 29°01′E], 20 December 1980, M. Stiller, on hill, under large granite rock lying on rock face, many millipede (Juliform) and beetle remains; ♀ (NMSA 13931), same data, except 18 December 1980; ♂ (TMSA 12507), Farm Boekenhoutskloofdrift 286 [25°18′S, 29°01′E], 20 September 1982, E. Voigt. Groblersdal district: 2♂, 2♀, 2 subadult ♀, juv ♂ (SAMC C4603), 20 km S of Groblersdal on road to Middelburg, 25°20.30′S, 29°22.85′E, 13 January 2000, L. Prendini & I. Engelbrecht, mixed bushveld, crevices in granite rocks, 1077 m. Middelburg district: 2♂ (TMSA 17458, 17513), Farm Noupoort 16, Selons River [25°25′S, 29°28′E], 1933; ♂, 5♀, juv ♂ (SAMC C4600), ♂, ♀ (CASC), 2 juv ♀ (AMC), 55 km S of Groblersdal on road to Middelburg, 25°32.27′S, 29°28.67′E, 13 January 2000, L. Prendini & I. Engelbrecht, grassland and mixed bushveld, crevices in sandstone, 1509

m; 2♂, 12♀ (SAMC C4601), ♂, ♀ (AMNH), Fort Merensky, Botshabelo Nature Reserve, 25°41.82′S, 29°24.87′E, 14 January 2000, L. Prendini & I. Engelbrecht, grassland, with mixed bushveld along banks of Olifants River, under flat stones and in crevices (sandstone), 1410 m. Witbank district: 2♀ (SAMC C4596), 2-D Ranch [Loskop Dam Nature Reserve], 25°22.101′S 29°18.409′E, October 1989, L. Prendini & M.R. Filmer, in crevices, 1070 m; ♀, juv ♀ (SAMC C4595), ♀ (SAMC C4598), 2-D Ranch [Loskop Dam Nature Reserve], 25°22.10′S, 29°18.41′E, October 1994, I. Engelbrecht, in crevices, 1070 m; ♀ (SAMC C4599), same data, except N. McLean; subadult ♂ (SAMC C4594), same data, except J. Laing; ♀, subadult ♂ (SAMC C4597), Amaphi Nature Reserve, on road from Loskop Dam to Verena, 25°21.66′S 29°18.69′E, 14 January 2000, L. Prendini & I. Engelbrecht, mixed bushveld, in crevices in granite, 1102 m.

Etymology.—The species name refers to the unusually long, slender pedipalps of the adult ♂.

Diagnosis.—*Hadogenes longimanus* is the sister species of *H. bicolor*. These two species are both characterized by a pronounced lobe, distal to the notch in the fixed finger of the pedipalp chela of adult ♂ and ♀, and a relatively short metasoma in the adult ♂, compared with *H. newlandsi* and other *Hadogenes* species. Accordingly, these characters are hypothesized to be synapomorphic for *H. bicolor* and *H. longimanus*.

Hadogenes longimanus can be distinguished from *H. bicolor*, and from *H. newlandsi*, by the presence of 5–8 trichobothria on the internal surface of the pedipalp chela. In both *H. bicolor* and *H. newlandsi*, there are only two *i* trichobothria on the chela.

Description.—The following description, which complements Hewitt's (1918) description of the ♂ from Doornkop, near Belfast, is based on the holotype ♂ (SAMC C4602; Figs. 11, 12), a paratype ♀ from 20 km S of Groblersdal (SAMC C4603; Figs. 13, 14), and a paratype ♂ and ♀ from Botshabelo (SAMC C4601), with differences between these specimens being noted.

Color: (SAMC C4602; SAMC C4603). Legs and tergites I-VI slightly paler, but not contrasting markedly with pedipalps, carapace, tergite VII and metasoma. Telson not distinctly paler than metasomal segments I-V.
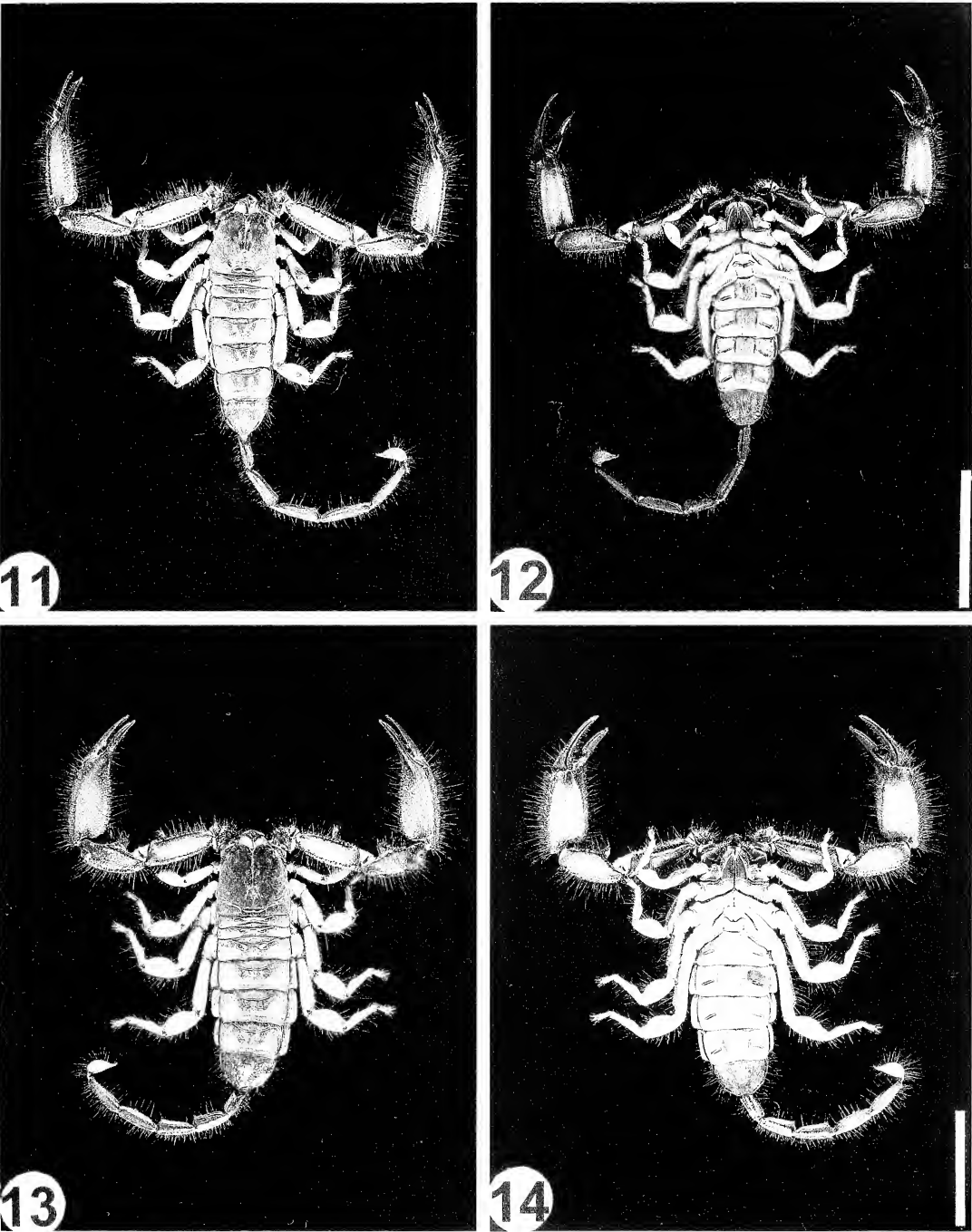
Figures 11–14.—***Hadogenes longimanus*** new species, habitus of holotype ♂ (SAMC C4602) and paratype ♀ (SAMC C4603). 11. Dorsal aspect, ♂; 12. Ventral aspect, ♂; 13. Dorsal aspect, ♀; 14. Ventral aspect, ♀. Scale bars = 20 mm.

Sternites distinctly paler than tergites and metasoma. Carapace, Amber 36 (♂) to Burnt Sienna 132 (♀); pedipalps, Amber 36 (♂) to Burnt Sienna 132 (♀) on chela manus and in-tercarinal surfaces of patella and femur, Sepia 119 on carinae and chela fingers; legs (except prolateral surfaces of femora) and tergites I-VI, Drab 27; cheliceral manus, tergite VII, and

metasoma, Fawn Color 25 (♂) to Burnt Sienna 132 (♀); cheliceral fingers and prolateral surfaces of leg femora, Sepia 119; sternites, pectines, and genital operculum, Sulphur Yellow 57.

Carapace: As for *H. bicolor*, with median notch in anterior margin slightly less pronounced.

Chelicerae: As for *H. bicolor*.

Pedipalps: As for *H. bicolor*, but differing in the following respects. Femur length 63.5% (60–67%) greater than width in ♂, 61.5% (61–62%) greater in ♀ (Table 2). Patella length 45% (42–48%) greater than width in ♂, 42.5% (42–43%) greater in ♀. Chela length along ventroexternal carina 49% (44–54%) greater than chela width in ♂, and 40.5% (40–41%) greater in ♀; chela width 47% (40–54%) greater than chela height in ♂, and 47.5% (46–49%) greater in ♀; length of movable finger 5% (2–8%) less than length along ventroexternal carina in ♂, and 4.5% (1–9%) less in ♀.

Trichobothria: Neobothriotaxic major, type C (Figs. 15–21), with the following segment totals (Table 2): femur 3 (1 *d*; 1 *i*; 1 *e*), patella 84–108 (2 *d*; 1 *i*; 28–43 *v*; 53–62 *e*) and chela 86–105 (73–89 manus; 13–16 fixed finger, including 5–8 *i*). Total number of τ per pedipalp, 173–216. Only femoral τ, τ in the *d* and *i* series of the patella, and τ in the *D*, *d*, and *e* series of the chela are stable in number and distribution. External and ventral τ of the chela and patella are numerically and distributionally too variable for diagnostic purposes. However, this species is characterized by the presence of accessory τ in the *i* series of the chela.

Mesosoma: Tergites each with paired submedian depressions and obsolete median carina. Pre-tergites of ♂ and ♀ smooth and shiny. Post-tergites I-VI smooth and shiny in ♂, except for very fine and even granulation on medial surfaces (excluding median carina and submedian depressions, which are smooth); post-tergite VII uniformly and finely granular in ♂; post-tergites of ♀ smooth and shiny. Sternites smooth and shiny, each with paired longitudinal depressions internal to spiracles. Sternite VII without posterolateral oval depressions, carinae, or notch in distal apex. Sternite VII 15.5% (13–18%) wider than long in ♂, 29.5% (29–30%) wider than long in ♀ (Table 2).

Pectines: As for *H. bicolor*, except pectinal teeth: 22–23/22–23 (♂), 16–19/15–19 (♀).

Sternum: As for *H. bicolor*.

Genital operculum: As for *H. bicolor*.

Legs: As for *H. bicolor*.

Metasoma and telson: As for *H. bicolor*, but metasomal segments shorter and more slender, with the following morphometric differences. Metasomal segment I 17% (10–24%) wider than high posteriorly (Table 2). Metasomal segments I-V progressively increasing in length, and decreasing in width, with segment V 30% (22–38%) narrower than segment I. Metasoma slender, width percentage of length for segment I, 45% (40–50%) in ♂, 47.5% (46–49%) in ♀; for II, 26% (23–29%) in ♂, 32% (30–34%) in ♀; for III, 23.5% (21–26%) in ♂, 29% (28–30%) in ♀; for IV, 20.5% (20–21%) in ♂, 26.5% (26–27%) in ♀; and for V, 17.5% (16–19%) in ♂, 24% (22–26%) in ♀. Telson vesicle 15% (14–16%) wider than metasomal segment V in ♂, 3.5% (2–5%) wider in ♀; oval in shape, with flattened dorsal surface and rounded ventral surface, height 37% (35–39%) of length. Aculeus short, 21.5% (19–24%) of vesicle length in ♂ and ♀, and sharply curved (Fig. 34). Total length of metasoma 9% (3–15%) longer than combined length of prosoma and mesosoma in ♂, but 13.5% (11–16%) shorter in ♀.

Hemispermatophore: Similar to that of *H. bicolor*, but teeth of doubled hook noticeably shorter (Fig. 37).

Geographic variation: Specimens from the Olifants River system (Bronkhorstspruit, Groblersdal, Middelburg and Witbank districts) are all very similar morphologically, although a general decrease in size occurs with increase in elevation from north to south in the distributional range. However, four specimens from Steelpoort (Lydenburg district), *ca.* 100 km northeast of the northernmost locality record in the Groblersdal district (Fig. 1), and the ♂ specimen from Doornkop (Carolina district), described by Hewitt (1918), differ from the typical form in several respects. The pedipalps, especially of the ♂, are proportionally shorter and broader, the carapace, post-tergites and metasoma are slightly more granular, and the trichobothrial counts are higher (total number of τ per pedipalp, 201–225).

Morphometric ratios of the pedipalps of a ♂ and ♀ from Steelpoort (Table 2) that differ from typical specimens are as follows: femur

length 57% greater than width in ♂, 55% greater in ♀; patella length 41% greater than width in ♂ and ♀; chela length along ventroexternal carina 39% greater than chela width in ♂, and 35% greater in ♀; length of movable finger 1% greater than length along ventroexternal carina in ♂, and 2% greater in ♀.

Unfortunately, the absence of any specimens from the area between these localities prevented an assessment of whether this variation is continuous or discrete. Further investigation, including the collection of additional material, will be required to determine if this variation has an ecological basis, or if these specimens represent yet another cryptic species in this complex. In light of this possibility, these five specimens have not been designated as paratypes of *H. longimanus*, and are thus listed below as "Material examined."

Ontogenetic variation: As for *H. bicolor*.

Sexual dimorphism: As for *H. bicolor*, except in this species the lobe distal to the notch in the fixed finger of the pedipalp chela is more pronounced in adult ♀ (Fig. 19), compared with adult ♀ *H. bicolor* (Fig. 9).

Chromosome number: Unknown.

Remarks: Electrophoretic data presented for *H. bicolor* from Zusterstroom (Bronkhorstspruit district, Gauteng Province) by Newlands (1980) and Newlands & Cantrell (1985) was derived from specimens that are conspecific with *H. longimanus* (e.g., TMSA 17452, 17453, 17460).

Distribution.—*Hadogenes longimanus* is endemic to a series of rocky outcrops and mountain ranges in the Gauteng and Mpumalanga provinces of South Africa (Fig. 1). Most of the known localities fall within the square bounded by 25–26°S latitude and 29–30°E longitude, and occur at an elevation between 1100–1500 m. However, *H. longimanus* has been collected below 1100 m in the Groblersdal district (Mpumalanga Province). The distributional range of this species coincides roughly with the upper reaches of the Olifants River and its tributaries, and is bounded by the Springbokvlakte plain (below 1000 m) to the north and west, and the Drakensberg escarpment (above 1500 m) to the south and east. The Springbokvlakte provides a natural barrier between *H. longimanus* and *H. newlandsi*, which occurs at lower elevation to the north of this plain. *Hadogenes bicolor* occurs at higher elevation than *H. longimanus* in the Drakensberg escarpment to the northeast.

Ecology.—In common with all other species of *Hadogenes*, *H. longimanus* is an obligately lithophilous scorpion. It inhabits the narrow cracks and crevices of weathered sandstone and granite rocks, and has also been collected from under large flat rocks resting on bedrock.

Below 1100 m, *H. longimanus* occurs in Mixed Bushveld (Van Rooyen & Bredenkamp 1996a), receiving a rainfall of 350–650 mm annually. However, above 1100 m, the species occurs in Rocky Highveld Grassland, receiving an annual rainfall of 650–750 mm (Bredenkamp & Van Rooyen 1996).

This species is sympatric with *Opistophthalmus glabrifrons* and *Uroplectes triangulifer* throughout most of its range. Prey remains in the crevices inhabited by these scorpions commonly included the rings of spirobolid and harpagophorid millipedes (Myriapoda), and the elytra of tenebrionid beetles (Coleoptera).

Conservation status.—*Hadogenes longimanus* is faced with the same threats as other *Hadogenes* species but, like *H. bicolor*, is comparatively less vulnerable for the following reasons. Firstly, it occurs mainly in regions of sedimentary geology, and less commonly on granite outcrops, and is thus less vulnerable to habitat destruction by the quarry-stone industry. Secondly, the distributional range of this species coincides with areas of high ecotourism potential in the Mpumalanga Province, and a considerable portion is already protected within existing parks. Viable populations have been recorded from the Loskop Dam and Botshabelo nature reserves, but additional populations probably exist within other reserves in the region.

Material examined.—SOUTH AFRICA: *Mpumalanga Province:* Carolina district: ♂ (AMGS), Doornkop, near Belfast, 25°55'S, 30°16'E, R. Gerhardt. Lydenburg district: 2♂ (SAMC C4275, 4276), ♀ (SAMC C4281), juv ♂ (SAMC C3901), Steelpoort, 24°43'S, 30°12'E, J. Visser.

***Hadogenes newlandsi* new species**
Figs. 1, 22–32, 35, 38, Table 2

Hadogenes bicolor Purcell 1899: Hewitt 1918: 160, 161 (part); Lamoral & Reynders 1975: 538 (part); Newlands 1980 (unpublished): 99–105 (part), fig.

Table 2.—Meristic data for adult ♂ and ♀ *Hadogenes bicolor* Purcell 1899, **Hadogenes longimanus** new species and **Hadogenes newlandsi** new species. Measurements following Stahnke (1970), Lamoral (1979) and Newlands & Prendini (1997). [1] Measured from base of condyle to tip of fixed finger. [2] Sum of metasomal segments I–V and telson.

Specimen:		*Hadogenes bicolor* Purcell					
	Sex	♂	♀	♂	♀	♂	♀
	Collection	SAMC	SAMC	TMSA	TMSA	SAMC	SAMC
	Number	4062	4062	18004	18005	C4585	C4585
	Type	lecto	paralecto				
Carapace:	anterior width	7.54	8.28	8.12	8.82	9.22	10.49
	posterior width	12.78	13.67	13.85	14.08	16.12	17.02
	length	12.70	13.37	13.33	14.20	16.10	16.59
Chela:	maximum width	7.59	8.55	7.78	9.90	9.73	11.00
	maximum height	3.29	4.28	3.76	4.56	5.47	5.66
	length[1]	25.86	27.30	27.99	29.18	34.12	31.69
	length of ventroexternal carina	13.61	14.14	15.28	15.77	18.22	16.36
	length of movable finger	12.84	13.65	13.29	14.72	16.24	16.26
	i trichobothria (left/right)	2/2	2/2	2/2	2/2	2/2	2/2
	E trichobothria (left/right)	39/40	36/39	35/35	34/35	37/38	34/39
	V trichobothria (left/right)	34/33	42/36	37/37	34/39	35/38	37/35
Patella:	maximum width	7.28	7.85	7.75	8.28	9.22	9.17
	maximum height	3.86	4.06	3.89	4.19	5.34	5.12
	length	13.28	13.15	13.92	14.23	16.97	15.24
	e trichobothria (left/right)	57/57	59/56	42/38	53/54	53/54	56/55
	v trichobothria (left/right)	34/31	31/30	31/30	29/29	27/28	30/31
Femur:	maximum width	5.28	5.64	5.64	5.59	6.98	6.83
	maximum height	2.99	3.39	3.28	3.27	4.45	4.13
	length	14.50	14.14	15.82	14.97	18.55	16.23
Pedipalp:	total length (including trochanter)	58.34	60.00	63.61	64.45	76.23	70.41
Mesosoma:	total length (tergites)	34.28	36.11	33.97	38.86	43.19	47.10
Sternite VII:	width	8.63	10.76	9.66	10.63	11.54	14.07
	length	7.87	8.11	7.37	8.51	9.94	9.46
Metasoma I:	maximum width	3.21	3.28	2.73	3.24	4.14	3.96
	maximum height	2.48	2.28	2.45	2.68	3.27	3.13
	length	7.49	6.11	7.46	6.43	9.83	7.05
Metasoma II:	maximum width	2.27	2.23	2.16	2.28	3.01	2.83
	maximum height	3.38	2.80	2.99	3.24	4.03	4.12
	length	9.52	7.27	9.56	7.10	12.60	9.02
Metasoma III:	maximum width	2.09	2.10	2.10	2.14	2.61	2.72
	maximum height	3.36	2.84	2.88	3.11	4.08	3.86
	length	9.96	7.33	9.98	7.53	12.92	9.38
Metasoma IV:	maximum width	1.96	2.04	1.91	2.12	2.52	2.51
	maximum height	2.84	2.72	2.80	2.93	3.67	3.63
	length	10.55	8.02	10.57	7.57	13.92	9.76
Metasoma V:	maximum width	2.06	2.02	1.82	2.03	2.50	2.54
	maximum height	2.79	2.48	2.68	2.65	3.39	3.24
	length	11.18	8.81	11.09	8.41	14.51	10.76
Telson:	maximum width	2.31	2.20	2.18	2.13	2.75	2.60
	maximum height	2.57	2.61	2.79	2.81	3.42	3.41
	aculeus length	1.84	1.61	1.68	1.86	2.38	2.13
	total length	7.77	7.52	7.98	7.59	9.34	8.78
Metasoma:	total length[2]	56.47	45.06	56.64	44.63	73.12	54.75
Total length:	prosoma + mesosoma + metasoma	103.45	94.54	103.94	97.69	132.41	118.44
Pectines:	total length	8.29	7.20	8.72	7.36	9.68	8.34
	length along dentate margin	7.53	6.03	8.13	6.21	8.30	6.61
	tooth count (left/right)	19/18	16/15	20/20	16/16	19/18	17/16

Table 2.—Extended.

Hadogenes longimanus new species						*Hadogenes newlandsi* new species			
♂ SAMC C4602 holo	♀ SAMC C4603 para	♂ AMNH para	♀ AMNH para	♂ SAMC C4275	♀ SAMC C4281	♂ SAMC C4589 holo	♀ SAMC C4593 para	♂ SAMC C4586 para	♀ SAMC C4586 para
9.97	9.48	7.76	8.01	9.89	11.64	9.40	10.00	8.92	9.47
15.80	15.51	12.49	12.83	16.04	18.58	15.43	16.81	14.43	15.63
15.57	15.34	12.36	12.74	16.07	19.11	16.13	16.60	14.87	15.53
8.62	9.76	7.63	8.03	10.13	12.11	10.22	11.26	9.25	10.46
5.17	5.00	3.49	4.30	5.35	6.47	5.13	5.72	4.39	4.82
34.49	31.63	25.94	25.00	32.07	36.52	31.25	32.89	26.66	28.42
18.71	16.30	13.82	13.50	16.57	18.68	16.95	17.69	13.59	15.26
18.15	16.28	12.77	12.34	16.75	19.01	16.03	17.60	13.52	14.50
6/5	5/5	7/6	6/5	6/6	7/8	2/2	2/2	2/2	2/2
37/39	40/43	39/39	39/38	39/36	41/44	30/34	32/30	30/29	33/34
34/36	42/38	44/46	38/38	47/45	46/49	33/35	33/34	34/37	33/36
9.06	8.80	7.19	7.08	8.96	10.36	8.70	9.72	8.17	8.64
4.57	4.66	3.58	3.80	5.37	5.79	4.78	5.23	4.35	4.58
17.56	15.52	12.34	12.27	15.12	17.64	15.15	15.54	13.06	13.51
56/55	62/60	54/53	54/57	73/70	69/70	41/49	52/48	48/50	52/51
28/32	33/33	34/33	43/39	37/36	33/31	29/28	29/31	29/31	30/32
6.56	6.35	5.50	5.04	6.68	8.03	6.78	7.31	6.58	6.41
4.15	4.04	3.13	3.18	4.02	5.19	4.24	4.38	3.50	3.72
20.10	16.55	13.87	13.02	15.64	18.00	15.76	16.04	13.60	14.19
79.36	70.56	58.11	56.00	68.83	80.76	68.92	71.51	59.41	62.75
44.35	42.20	37.67	36.17	46.84	55.17	50.68	47.58	41.27	44.25
12.10	12.26	9.67	10.88	11.77	13.86	12.26	13.88	10.56	12.17
9.90	8.61	8.40	7.75	10.00	11.05	10.83	10.38	10.08	9.48
3.46	3.04	3.19	2.79	3.43	3.96	4.11	3.95	4.08	3.68
3.11	2.99	2.43	2.42	3.14	3.30	3.66	3.24	2.81	2.84
8.58	6.58	6.38	5.66	9.77	8.58	12.24	7.86	10.25	7.26
2.87	2.57	2.44	2.43	2.73	2.84	3.02	2.84	2.84	2.90
3.73	3.41	3.13	3.21	3.75	4.06	4.83	4.00	3.95	3.42
12.24	8.44	8.54	7.16	12.34	10.85	16.22	10.10	13.88	9.32
2.69	2.44	2.37	2.15	2.48	2.88	2.92	2.69	2.71	2.63
3.58	3.42	3.09	3.00	3.72	4.16	4.53	4.03	3.85	3.52
12.69	8.73	9.20	7.28	12.64	11.17	16.29	10.09	14.63	9.35
2.66	2.43	2.12	2.03	2.48	2.69	2.73	2.57	2.33	2.24
3.15	2.98	2.68	2.72	3.10	3.54	3.88	3.73	3.23	2.99
13.41	9.27	9.95	7.59	13.15	12.08	17.43	11.05	15.46	10.38
2.42	2.37	1.97	1.97	2.31	2.63	2.52	2.67	2.28	2.17
3.19	2.81	2.51	2.35	3.03	3.38	3.76	3.63	2.92	2.67
14.69	10.57	10.61	7.61	13.49	12.53	17.29	11.60	15.81	10.54
2.89	2.50	2.30	2.01	2.47	3.16	2.95	2.90	2.47	2.23
3.37	2.82	2.82	2.55	3.08	3.48	3.68	3.57	3.26	2.71
2.17	1.96	1.37	1.44	2.12	2.92	1.73	2.32	1.79	1.94
9.17	8.12	7.14	6.74	8.71	10.33	10.01	9.22	8.63	8.10
70.78	51.71	51.82	42.04	70.10	65.54	89.48	59.92	78.66	54.95
130.70	109.25	101.85	90.95	133.01	139.82	156.29	124.10	134.80	114.71
11.10	8.49	9.38	6.84	12.23	9.50	10.77	8.62	8.48	7.62
10.29	7.34	8.47	5.59	11.84	7.84	10.25	6.98	8.11	5.80
23/23	19/19	22/22	16/15	24/23	18/18	21/22	17/16	23/21	18/16

15

16 17 18
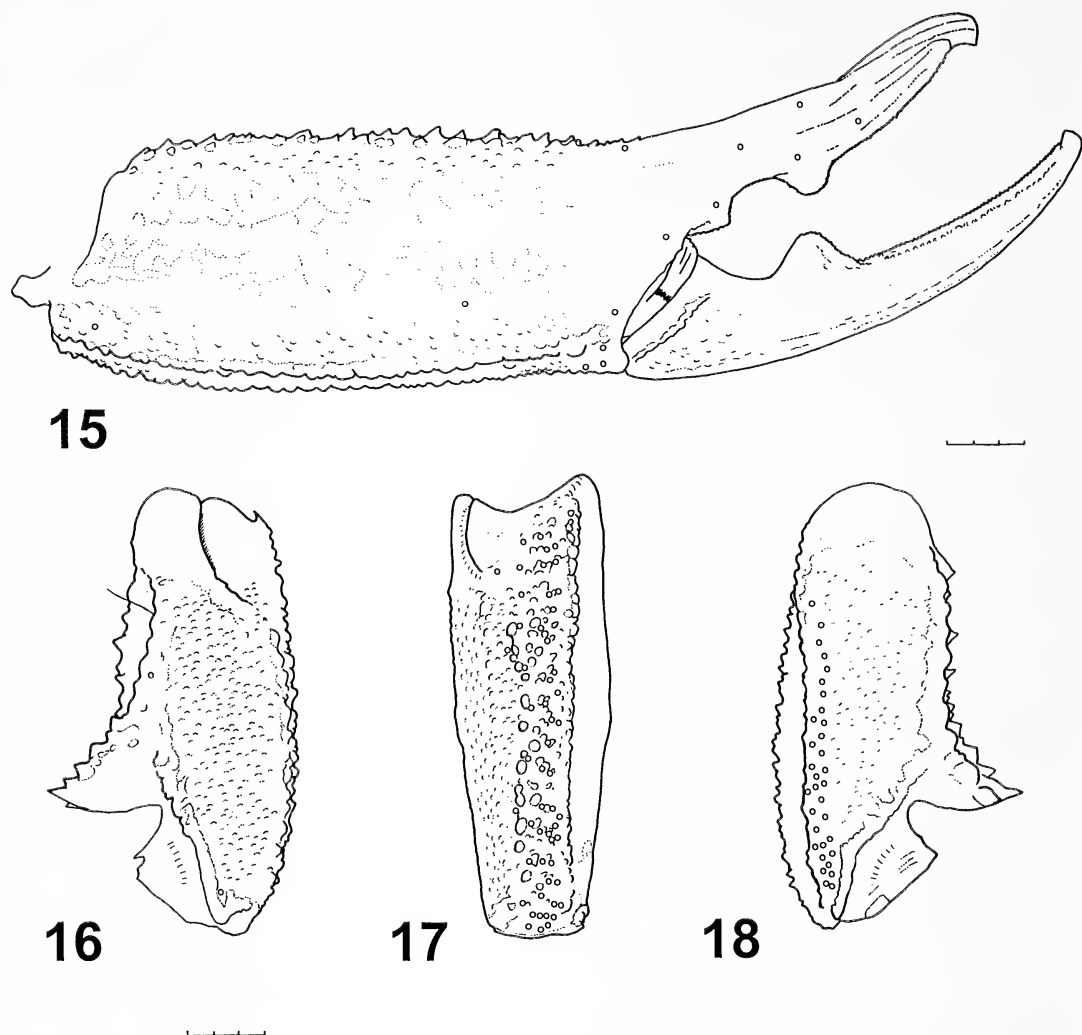
Figures 15–18.—*Hadogenes longimanus* new species, dextral pedipalp segments of holotype ♂ (SAMC C4602) and paratype ♀ (SAMC C4603), showing trichobothrial distribution and shape of lobes on fixed and movable fingers of the chela. 15. Dorsal aspect of chela, ♂; 16. Dorsal aspect of patella, ♀; 17. External aspect of patella, ♀; 18. Ventral aspect of patella, ♀. Scale bars = 3 mm.

48 (part); Newlands & Cantrell 1985: 40, 42, 44 (part).

Types.—SOUTH AFRICA: *Northern Province:* Holotype ♂ (SAMC C4589), Soutpansberg district: Ben Lavin Nature Reserve, 23°07.544′S, 29°56.573′E, 31 December 1999, L. Prendini & E. Scott, in crevices in granite rocks, mixed bushveld, 850 m. Paratypes: Letaba district: subadult ♂ (TMSA 12565), Letsitele, Tzaneen [23°53′S, 30°24′E], 21 September 1964, R.D. Faul; 2♂ (TMSA 114, 117), 10♀ (TMSA 112, 113, 115, 116, 118–122, 125), 2 juv ♀ (TMSA

127, 128), Mooketsi [23°35′S, 30°03′E], April 1924, G.P.F. van Dam. Pietersburg district: subadult ♂ (TMSA 1057), Clearwaters, Haenertsburg [23°51′S, 29°57′E], 4 February 1916, G.A. Thompson; subadult ♀ (TMSA 1058), Farm Munniks [23°37′S, 29°57′E], 16 January 1914, Pienaar; ♀ (AMNH), Pietersburg area [23°54′S, 29°27′E]; ♀ (TMSA 1055), Woodbush [23°47′S, 29°54′E], December 1907, D. Gough; subadult ♂ (AMGS 3990), The Woodbush. Potgietersrus district: juv ♀ (TMSA 2184), Potgietersrus [24°11′S, 29°01′E], 27 March 1919, H.B. Pretorius; juv
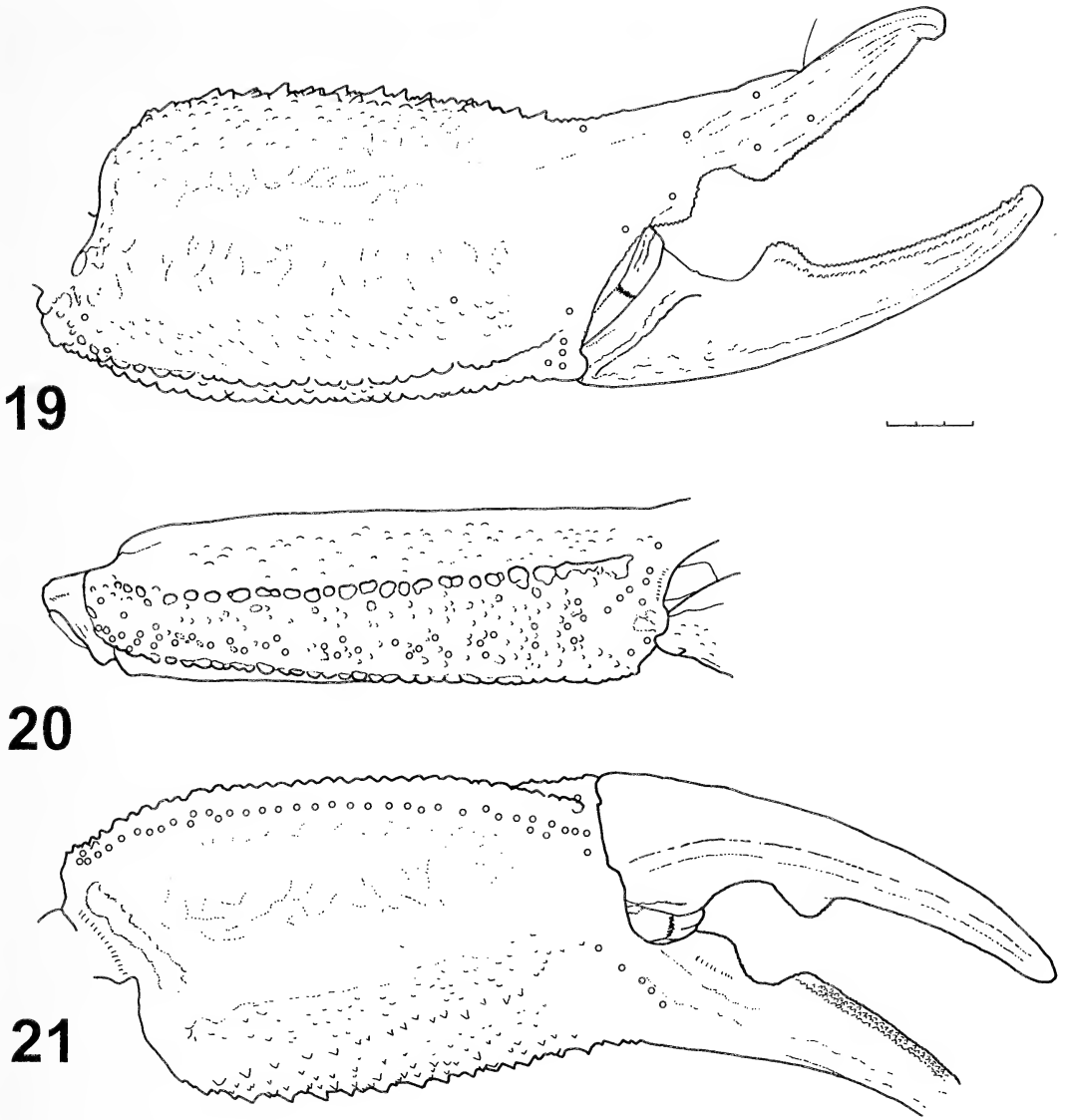
Figures 19–21.—***Hadogenes longimanus*** new species, dextral pedipalp chela of paratype ♀ (SAMC C4603), showing trichobothrial distribution and shape of lobes on fixed and movable fingers. 19. Dorsal aspect; 20. External aspect; 21. Ventrointernal aspect. Scale bar = 3 mm.

♀ (TMSA 6108), Maribashoek [24°13′S, 29°08′E], December 1924, G.P.F. van Dam; ♂ (TMSA 10484), 3♀ (TMSA 10481–10483), juv ♂ (TMSA 10485), Percy Fife Nature Reserve [24°02′S, 29°11′E], 11 May 1972, N.H.G. Jacobsen; subadult ♀ (TMSA 20393), Potgietersrus Nature Reserve [24°09′S, 28°59′S], 11 May 1972, N.H.G. Jacobsen; juv ♀ (TMSA 708), Makapan Caves [24°09′S, 29°11′E], 4 February 1911, A. Roberts; juv ♂ (TMSA 10781), Makapansgat, 31 August 1973, R. Clark; ♀ (TMSA 17451), juv ♀ (TMSA 17450), Makapansgat, I.H. Davidson; ♀ (AMC), Makapansgat World Heritage Site, April 2000, I. Engelbrecht. Sekgosese district: 2♂, 9♀, juv ♂, juv ♀ (SAMC C4592), ♂, ♀ (CASC), juv ♂, juv ♀ (AMC), St. Brendan's Catholic School (Mission Matok), 23°25.63′S, 29°43.28′E, 29 December 1999, L. Prendini & E. Scott, mixed bushveld, granite outcrops, in crevices, 980 m; ♀, juv ♀ (SAMC C4591), Mphakane, south, granite koppies 1 km from turnoff to Munnik, 23°32.20′S, 29°42.42′E, 29 December 1999, L. Prendini & E. Scott, in
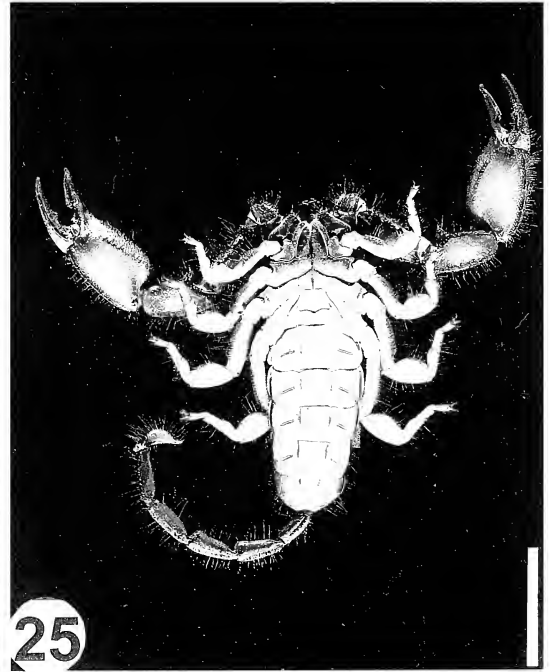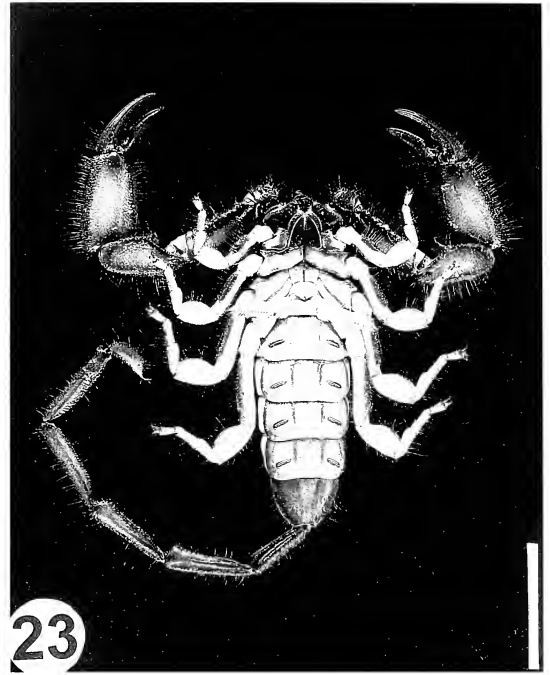
Figures 22–25.—***Hadogenes newlandsi*** new species. habitus of holotype ♂ (SAMC C4589) and paratype ♀ (CASC). 22. Dorsal aspect, ♂; 23. Ventral aspect, ♂; 24. Dorsal aspect, ♀; 25. Ventral aspect, ♀. Scale bars = 20 mm.

crevices in rock, 1000 m. Soutpansberg district: subadult ♂ (CASC), 10 mi S of Louis Trichardt, 25 March 1958, E.S. Ross & R.E. Leech, 1000 m; ♀, 3 juv ♂, juv ♀ (CASC), same data, except 18 mi S of Louis Trichardt; 2 juv ♀ (CASC), same data, except 35 mi S of Louis Trichardt, 26 March 1958; 2 ♀ (SAMC C4587), Bandelierkop, 23°18′S,
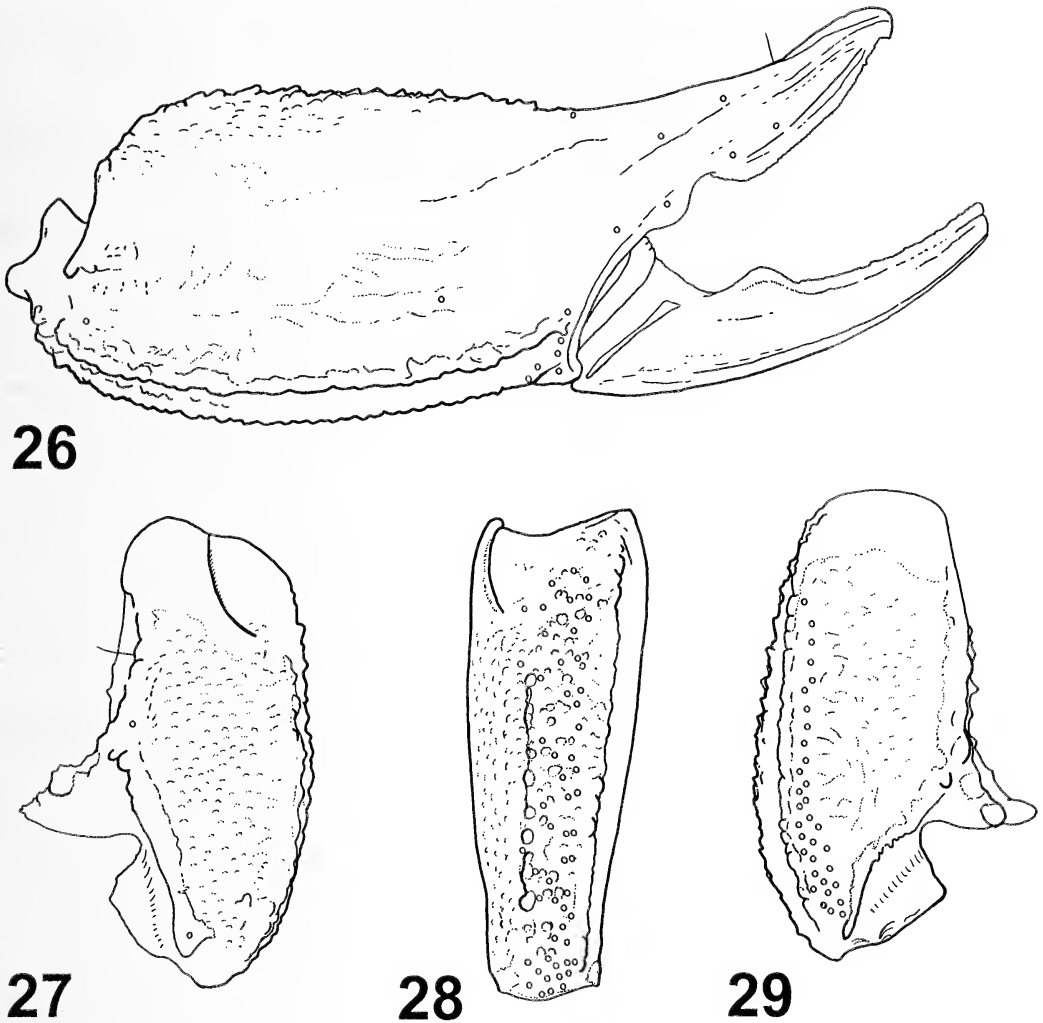
Figures 26–29.—**Hadogenes newlandsi** new species, dextral pedipalp segments of ♂ and ♀ paratypes (SAMC C4586), showing trichobothrial distribution and shape of lobes on fixed and movable fingers of the chela. 26. Dorsal aspect of chela, ♂; 27. Dorsal aspect of patella, ♀; 28. External aspect of patella, ♀; 29. Ventral aspect of patella, ♀. Scale bar = 3 mm.

29°51'E, April 1988, L. Prendini, M.R. Filmer, A.M. Smith & V. Hull-Williams, in crevices in granite koppie; ♂, ♀, juv ♂ (SAMC C4586), Bandelierkop, 1995, I. Engelbrecht; ♀, 2 juv ♀ (SAMC C4590), Mailaskop, 23°13.43'S, 29°56.63'S, 30 December 1999, L. Prendini & E. Scott, in crevices in dolerite rocks on koppie, 1124 m; ♂, ♀ (SAMC C4588), Tabajwane Koppie, Ben Lavin Nature Reserve, December 1990, L. Prendini & K.M.A. Prendini, in crevices in granite rocks, 970 m; 3♂, 5♀, subadult ♀ (SAMC C4593), ♂, ♀ (AMNH), Ben Lavin Nature Reserve, 23°07.544'S, 29°56.573'E, 31 December 1999, L. Prendini & E. Scott, in crevices in granite rocks, mixed bushveld, 850 m.

Etymology.—The new species is named in honor of Dr. Gerald Newlands for his contributions to the ecology and systematics of southern African scorpions in general and *Hadogenes* in particular.

Diagnosis.—*Hadogenes newlandsi* is most closely related to the group comprising *H. bicolor* and *H. longimanus*. In all three species, the distal width of metasomal segment I is greater than its height. *Hadogenes newlandsi* can be distinguished from the latter species by the absence of a pronounced lobe, distal to the

notch in the fixed finger of the pedipalp chela of adult ♂ and ♀, and by the longer metasoma of the adult ♂ (which is approximately the same length as the metasoma of certain other *Hadogenes* species, e.g., *H. gunningi*). *Hadogenes newlandsi* is further characterized by the presence, in adult ♂, of dense granulation on the telson and lateral surfaces of metasomal segment V. The latter character has proved consistent in separating *Hadogenes granulatus* Purcell 1901 from the morphologically similar *H. troglodytes*, which occur sympatrically in parts of Zimbabwe (Bergman 1995).

Description.—The following description is based on the holotype ♂ (SAMC C4589; Figs. 22, 23), two paratype ♀ from Ben Lavin (SAMC C4593, CASC; Figs. 24, 25), and a paratype ♂ and ♀ from Bandelierkop (SAMC C4586).

Color: (SAMC C4589; SAMC C4593). Pale legs contrasting markedly with darker pedipalps, carapace, tergites and metasoma. Telson not distinctly paler than metasomal segments I–V. Sternites distinctly paler than tergites and metasoma. Pedipalps, Tawny 38 on chela manus and intercarinal surfaces of patella and femur, Sepia 119 on carinae and chela fingers; cheliceral manus, carapace, tergites (♂) and metasoma, Hooker's Green 162; tergites (♀), Grayish Olive 43; legs (except prolateral surfaces of femora) of ♂, sternites, pectines and genital operculum, Straw Yellow 36; legs (♀), Tawny 38; cheliceral fingers and prolateral surfaces of leg femora, Sepia 119.

Carapace: As for *H. bicolor*, except median notch in anterior margin very weakly developed, and frontal lobes of ♂ almost entirely granular.

Chelicerae: As for *H. bicolor*.

Pedipalps: As for *H. bicolor*, but differing in the following respects. Femur length 54.5% (52–57%) greater than width in ♂ and ♀ (Table 2). Patella length 40% (37–43%) greater than width in ♂, 36.5% (36–37%) greater in ♀. Chela with a pronounced, conical lobe on movable finger and corresponding notch in fixed finger; fixed finger additionally with a small, rounded lobe proximal to the notch, but without a pronounced, conical lobe distally (Figs. 26, 30). Chela length along ventroexternal carina 35.5% (32–39%) greater than chela width in ♂, and 33.5% (31–36%) greater in ♀; chela width 51.5% (49–54%) greater

than chela height in ♂ and ♀; length of movable finger 3% (1–5%) less than length along ventroexternal carina in ♂ and ♀.

Trichobothria: Neobothriotaxic major, type C (Figs. 26–32), with the following segment totals (Table 2): femur 3 (1 *d*; 1 *i*; 1 *e*), patella 72–87 (2 *d*; 1 *i*; 28–32 *v*; 41–52 *e*) and chela 72–81 (62–71 manus; 10 fixed finger, including 2 *i*). Total number of τ per pedipalp, 147–171. Only femoral τ, τ in the *d* and *i* series of the patella, and τ in the *D*, *d*, *e* and *i* series of the chela are stable in number and distribution. External and ventral τ of the chela and patella are numerically and distributionally too variable for diagnostic purposes.

Mesosoma: Tergites each with paired submedian depressions and obsolete median carina. Pre-tergites of ♂ and ♀ smooth and shiny. Post-tergites of ♂ covered with very fine and even granulation, imparting a matte appearance to all surfaces, except median carina and submedian depressions, which are smooth; post-tergites of ♀ smooth and shiny. Sternites smooth and shiny, each with paired longitudinal depressions internal to spiracles. Sternite VII additionally with a pair of shallow posterolateral oval depressions (more prominent in ♂), and a pair of obsolete carinae, converging distally towards a shallow notch in distal apex. Sternite VII 8.5% (5–12%) wider than long in ♂, 23.5% (22–25%) wider than long in ♀ (Table 2).

Pectines: As for *H. bicolor*, except pectinal teeth: 21–23/21–22 (♂), 17–18/16 (♀).

Sternum: As for *H. bicolor*.

Genital operculum: As for *H. bicolor*.

Legs: As for *H. bicolor*.

Metasoma and telson: As for *H. bicolor*, except for the presence, in adult ♂, of more pronounced spiniform granules on metasomal segments II-V, and dense granulation on the lateral surfaces of segment V and telson (Fig. 35). In addition, metasomal segments of adult ♂ longer than in *H. bicolor*, with morphometric differences as follows. Metasomal segment I 21% (11–31%) wider than high posteriorly (Table 2). Metasomal segments I-V progressively increasing in length, and decreasing in width, with segment V 35% (29–41%) narrower than segment I. Metasoma slender, width percentage of length for segment I, 36.5% (34–39%) in ♂, 50.5% (50–51%) in ♀; for II, 19.5% (19–20%) in ♂, 29.5% (28–31%) in ♀; for III, 18.5% (18–
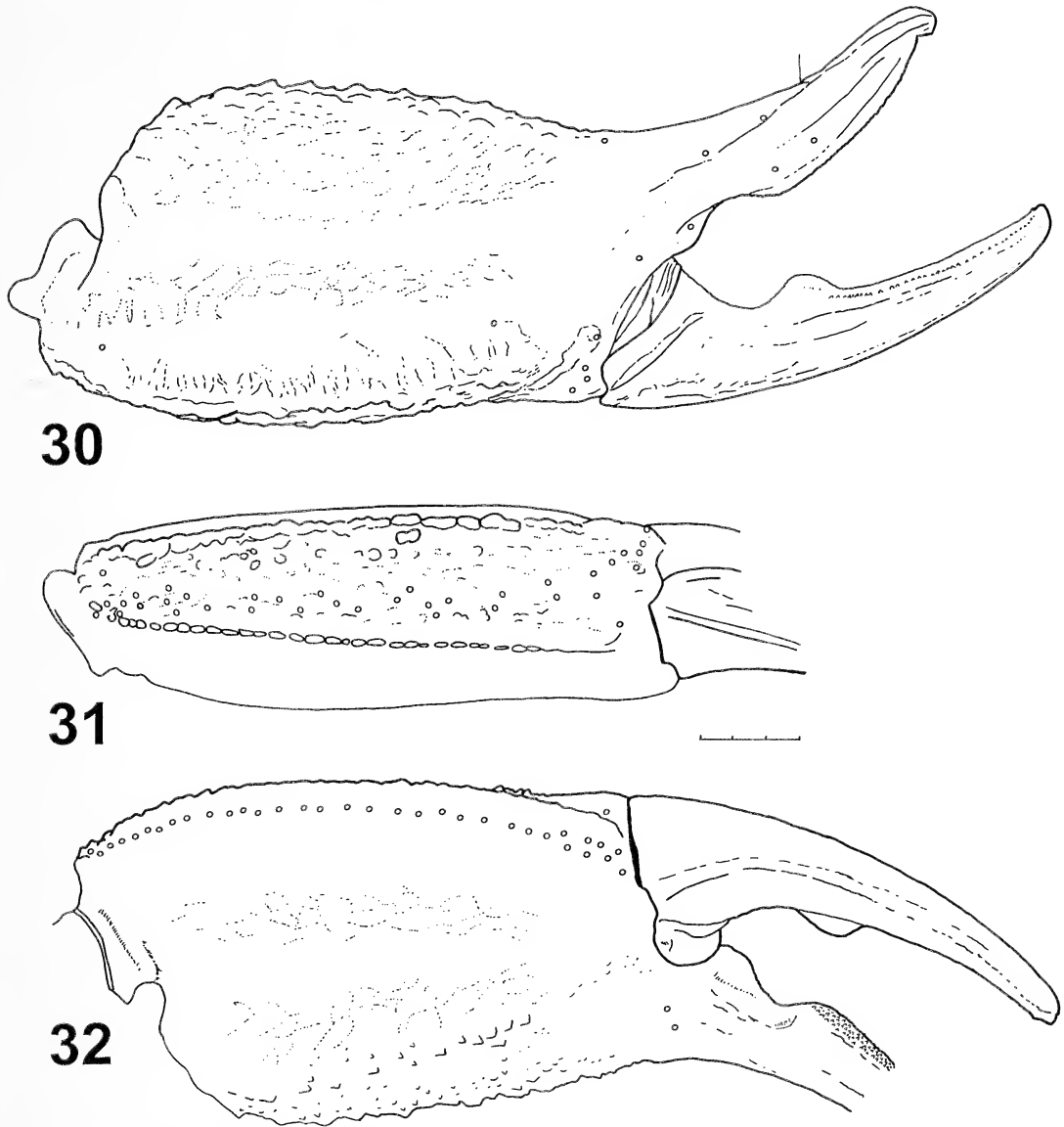
Figures 30–32.—***Hadogenes newlandsi*** new species, dextral pedipalp chela of paratype ♀ (SAMC C4586), showing trichobothrial distribution and shape of lobes on fixed and movable fingers. 30. Dorsal aspect; 31. External aspect; 32. Ventrointernal aspect. Scale bar = 3 mm.

19%) in ♂, 27.5% (27–28%) in ♀; for IV, 15.5% (15–16%) in ♂, 22.5% (22–23%) in ♀; and for V, 14.5% (14–15%) in ♂, 22.5% (22–23%) in ♀. Telson vesicle 11.5% (8–15%) wider than metasomal segment V in ♂, 5.5% (3–8%) wider in ♀; distinctly elongated in ♂, oval in ♀, with flattened dorsal surface and rounded ventral surface, height 36% (33–39%) of length. Aculeus short, 19% (17–21%) of vesicle length in ♂, 24.5% (24–25%) in ♀, and sharply curved. Total length of metasoma

27% (25–29%) longer than combined length of prosoma and mesosoma in ♂, but 8% (7–9%) shorter in ♀.

Hemispermatophore: Similar to that of *H. bicolor*, but teeth of doubled hook noticeably longer (Fig. 38).

Geographic variation: Little geographic variation besides a general decrease in size, associated with increase in elevation from north to south in the distributional range. Specimens from the southern part of the range
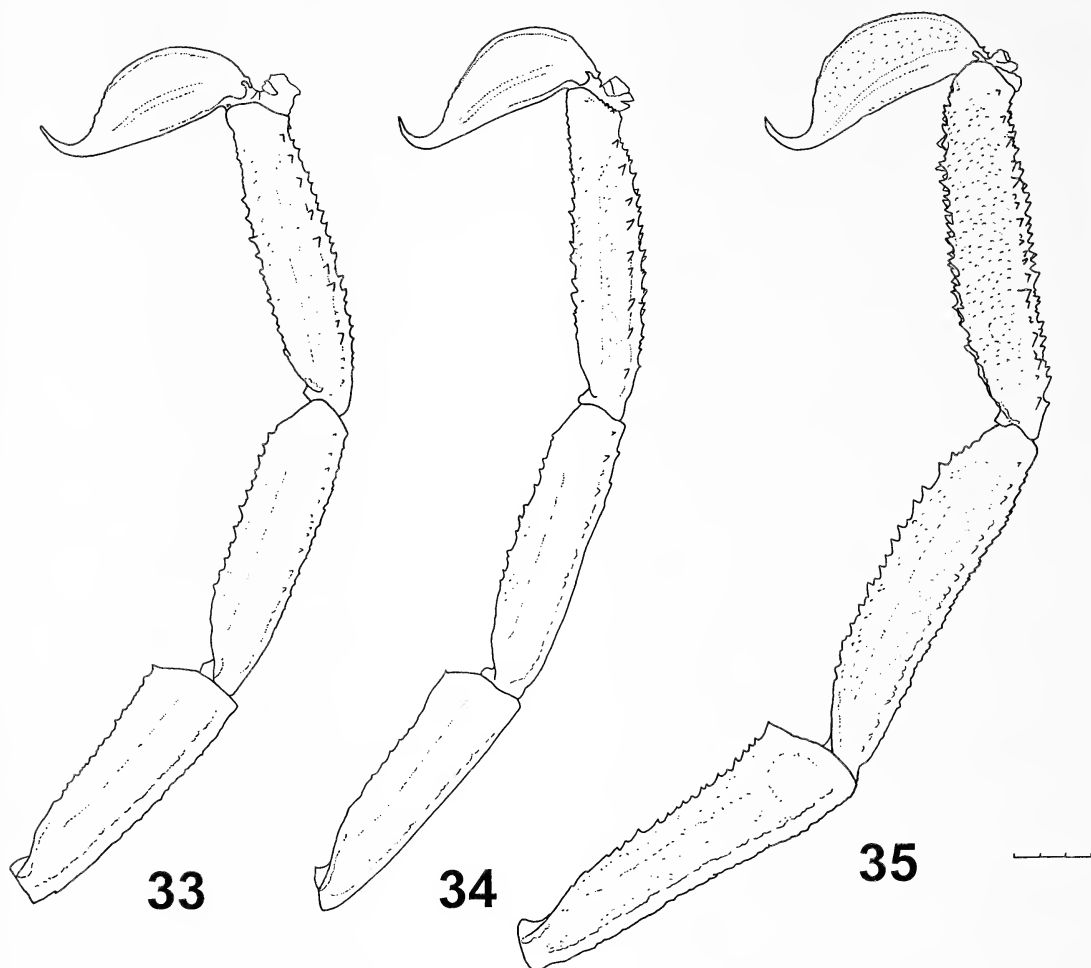
Figures 33–35.—Lateral aspect of metasomal segments III-V and telson, showing diagnostic differences in shape and granulation. 33. *Hadogenes bicolor* Purcell 1899 (♂, SAMC C4585); 34. **Hadogenes longimanus** new species (holotype ♂, SAMC C4602); 35. **Hadogenes newlandsi** new species (holotype ♂, SAMC C4589). Scale bar = 3 mm.

(e.g., Makapansgat) are also lighter in color, and have longer metasomal segments, than those from further north (e.g., Ben Lavin).

Ontogenetic variation: As for *H. bicolor.*

Sexual dimorphism: As for *H. bicolor,* except in this species the lobe on the movable finger of the pedipalp chela and notch in the fixed finger (no lobe is present distal to the notch), are equally pronounced in adult ♂ and ♀ (Figs. 26, 27), compared with adult ♂ and ♀ *H. bicolor* (Figs. 8, 9), and the metasoma of adult ♂ is considerably more elongated, with segment V and telson densely granular (Fig. 35).

Chromosome number: Unknown.

Remarks: The three specimens of *H. bicol-*

or from Woodbush, mentioned by Hewitt (1918), are conspecific with *H. newlandsi* (e.g., TMSA 1055, AMGS 3990).

Distribution.—*Hadogenes newlandsi* is restricted to inselbergs and mountain ranges in the Northern Province of South Africa (Fig. 1). Most locality records fall in the square bounded by 23–24°S latitude and 29–30°E longitude. Although specimens have been collected at an elevation between 800–1100 m in the northern part of the distributional range, locality records from the southern part of the distribution occur at an elevation between 1200–1500 m. The area of distribution is delimited by the Soutpansberg mountain range (above 1300 m) to the north, the Drakensberg

escarpment (above 1500 m) to the east, the Mogalakwena River Valley (below 900 m) to the west, and the Springbokvlakte plain (below 1000 m) to the south. The Springbokvlakte provides a natural barrier between *H. newlandsi* and *H. longimanus*, which occurs at higher elevation to the south of this plain. *Hadogenes bicolor* occurs at higher elevation than *H. newlandsi* in the Drakensberg escarpment to the southeast.

Ecology.—*Hadogenes newlandsi* is obligately lithophilous, inhabiting the narrow cracks, crevices and exfoliations of weathered granite and dolerite outcrops. It is restricted to Mixed Bushveld, receiving a rainfall of 350–650 mm annually (Van Rooyen & Bredenkamp 1996a).

In the rocky inselbergs that it inhabits, *H. newlandsi* is sympatric with *Parabuthus transvaalicus* and *Uroplectes olivaceus*. This species has also been collected in sympatry with *Cheloctonus jonesii* Pocock 1892 and *Opistophthalmus glabrifrons* at Bandelierkop and Ben Lavin. Prey remains in the crevices occupied by these scorpions included the rings of spirobolid millipedes (Myriapoda) and the elytra of carabid and tenebrionid beetles (Coleoptera).

Conservation status.—*Hadogenes newlandsi* is heavily threatened by habitat destruction for the quarry-stone industry. Many of the granite inselbergs inhabited by this species have been extensively quarried in the Pietersburg and Soutpansberg districts. Fortunately, the conservation status of *H. newlandsi* is assured by the existence of viable populations in the Percy Fife, Potgietersrus and Ben Lavin Nature Reserves, as well as at the Makapansgat World Heritage Site. The occurrence of the species in the Happy Rest, Kuschke and Pietersburg nature reserves, which also fall within its known distributional range, has not been verified, but seems probable.

DISCUSSION

The phylogenetic position of *Hadogenes* within the Ischnuridae was recently questioned by Lourenço (1999, 2000). Lourenço (1985, 1989, 1999) has consistently maintained that *Hadogenes* is the sister genus of *Heteroscorpion* Kraepelin 1905, the endemic Malagasy genus for which Lourenço (1996) erected the monotypic family Heteroscorpionidae Kraepelin 1905. Although it has never

been explicitly stated by Lourenço, the hypothesized relationship between *Hadogenes* and *Heteroscorpion* has presumably been adopted from Kraepelin (1896, 1899, 1901) and inferred from the following characters: the presence of accessory trichobothria in the *v* and *e* series of the pedipalp patella and in the *V* series of the pedipalp chela; the presence of an elongated, laterally compressed metasoma, particularly conspicuous in the adult male. These characters provided the primary justification for Kraepelin's (1896) original placement of the type species, *Heteroscorpion opisthacanthoides* (Kraepelin 1896), in the genus *Hadogenes*.

According to Kraepelin (1896: 137):

"Die cauda [of *H. opisthacanthoides*] ist weniger zusammengedrückt als bei der typischen Art [*Hadogenes*] *trichiurus*, zeigt aber noch die concaven Begrenzungslinien des Oberrandes der Segmente (Fig. 16 [illustrating lateral aspect of metasomal segments I-II]), welche für *Hadogenes* so charackterisch sind. Noch mehr endlich entfernt sich die Art von *Opisthacanthus* durch den Besitz einer Reihe von etwa zehn sehr deutlichen Haargruben am unteren Hinterrande des Unterarms (Fig. 18 [illustrating ventral aspect of right pedipalp patella]), denen eine ebenfalls scharf ausgeprägte dichte Reihe von Haargrübchen am Außenrande der Unterhand entspricht. Diese Bildungen schließen sich eng an die Vorkommnisse bei [*Hadogenes*] *tityrus* an, und da die stärkere oder schwächere Ausrandung der Stirn ebensowenig wie die stärkere oder schwächere Compression der Cauda oder die Abplattung des Körpers als generische Merkwale verwerthet werden können, so glaube ich die neue Art [*H. opisthacanthoides*] auf Grund eben jener Haargrübchenreihen der Gattung *Hadogenes* einreihen zu sollen."

In addition, all species of *Hadogenes* are characterized by the presence of a doubled hook on the hemispermatophore (Lamoral 1979). Lourenço (1999: 930) considered these characters to provide justification for the creation of a new subfamily Hadogeninae, which he transferred to the Scorpionidae:

"Lamoral (1979) dresse une liste des car-
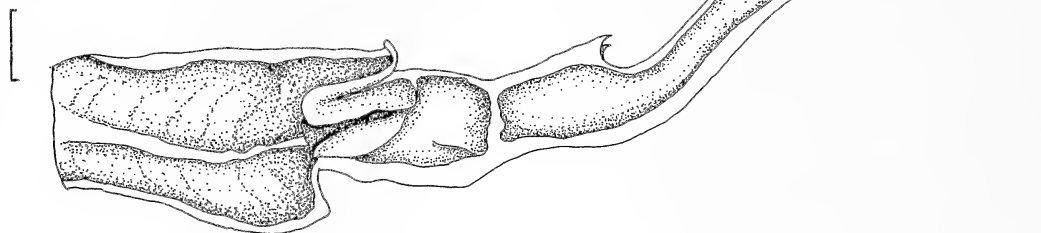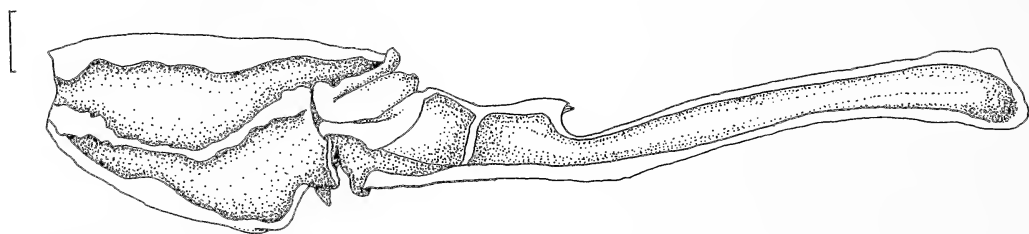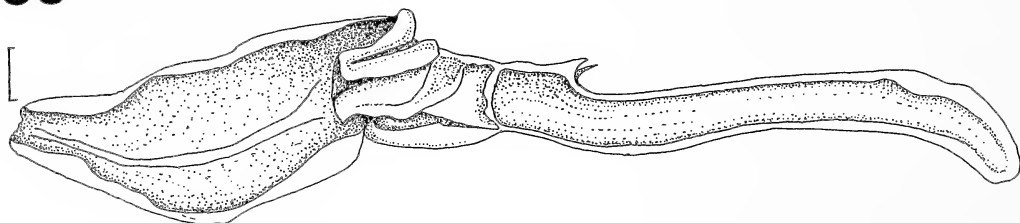
Figures 36–38. Left hemispermatophores. 36. *Hadogenes bicolor* Purcell 1899 (♂, TMSA 18004); 37. *Hadogenes longimanus* new species (paratype ♂, TMSA 17513); 38. *Hadogenes newlandsi* new species (paratype ♂, SAMC C4588). Scale bars = 1 mm.

actères différentiels entre le genre *Hadogenes* et les autres genres appartenant aux Ischnuridae, en particulier ceux tirés de la structure des hémispermatophores et du modèle trichobothriotaxique, caractères globalement négligés par les auteurs précédents déjà cités. Ces caractères sont réanalysés lors de l'étude réaliseé par Lourenço (1985, 1989), sans pour autant aboutir a une décision sur la position systématique des *Hadogenes*. A présent, un ensemble de caractères m'amène à proposer une nouvelle sous-famille monotypique avec genre-type *Hadogenes*. Cette

sous-famille est placée, par prudence, au sein de la famille des Scorpionidae."

Lourenço (2000: 26) subsequently elevated the Hadogeninae to Hadogenidae in a footnote, which states: "Les caractéristiques définissant les Hadogeninae sont exposées dans ma note de 1999."

Prendini (2000) falsified the hypothesis that *Hadogenes* is the sister genus of *Heteroscorpion* in a cladistic analysis that consistently placed *Hadogenes* within the Ischnuridae. Fourteen extra steps (17.5 decrease in fitness) were required to constrain (*Hadogenes* + *Het-*

eroscorpion) to be the monophyletic sister-group of the remaining ischnurid genera, as proposed by Lourenço (1985, 1989). Similarly, there was no evidence for a relationship between *Hadogenes* and the Scorpionidae. Optimization of the characters proposed for the Hadogenidae revealed that dorsoventral and lateral compression are plesiomorphic, the doubled hook of the hemispermatophore is autapomorphic, and both the elongated metasoma and the accessory trichobothria have been independently derived on numerous occasions within the Hemiscorpiidae Pocock 1893, Heteroscorpionidae, Ischnuridae and Scorpionidae (Prendini 2000). Provision of familial status for *Hadogenes* renders the Ischnuridae paraphyletic and is unjustified by the evidence. Accordingly, I hereby propose the new synonymy: Hadogenidae Lourenço 2000 = Ischnuridae Simon 1879.

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LITERATURE CITED

Bergman, N.J. 1995. Scorpionism in Zimbabwe. An Epidemiological and Clinical Investigation into Scorpionism in the Gwanda District of Zimbabwe, With Particular Reference to *Parabuthus transvaalicus* (Purcell). Unpubl. M.D. thesis. University of Zimbabwe. 300 pp.

Bredenkamp, G.J. & N. van Rooyen. 1996. Rocky highveld grassland. P. 39. *In* Vegetation of South Africa, Lesotho and Swaziland. (A.B. Low & A.G. Rebelo, eds.). Dept. Environmental Affairs & Tourism, Pretoria.

Bredenkamp, G.J., E. Granger & N. van Rooyen. 1996. North-eastern mountain grassland. Pp. 46–47. *In* Vegetation of South Africa, Lesotho and Swaziland. (A.B. Low & A.G. Rebelo, eds.). Dept. Environmental Affairs & Tourism, Pretoria.

Couzijn, H.W.C. 1976. Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments. Netherlands Journal of Zoology 26:453–501.

Fet, V. 2000. Family Ischnuridae. Pp. 383–408. *In* Catalog of the Scorpions of the World (1758–1998). (V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder). New York Entomol. Soc., New York.

Hewitt, J. 1918. A survey of the scorpion fauna of South Africa. Transactions of the Royal Society of South Africa 6:89–192.

Hjelle, J.T. 1990. Anatomy and morphology. Pp. 9–63. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford Univ. Press, Stanford, California.

Kovařík, F. 1998. Stirí (Scorpions en tchèque). Madagaskar, Jihlava.

Kraepelin, K. 1896. Neue und weniger bekannte Skorpione. Mitteilungen aus dem Naturhistorischen Museum (Beiheft zum Jahrbuch der Hamburgischen Wississenschaftlichen Anstalten) 13:119–146.

Kraepelin, K. 1899. Scorpiones und Pedipalpi. *In* Das Tierreich. (F. Dahl, ed.). 8:1–265. R. Friedländer, Berlin.

Kraepelin, K. 1901. Catalogue des scorpions des collections du Muséum d'histoire naturelle de Paris. Bulletin du Muséum National d'Histoire Naturelle, Paris 7:263–265.

Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). Annals of the Natal Museum 23:498–783.

Lamoral, B.H. & S.C. Reynders. 1975. A catalogue of the scorpions described from the Ethiopian faunal region up to December 1973. Annals of the Natal Museum 22:489–576.

Lawrence, R.F. 1955. Solifugae, scorpions and Pedipalpi, with checklists and keys to South Afri-

can families, genera and species. Results of the Lund University Expedition in 1950-1951. *In* South African Animal Life. (B. Hanström, P. Brinck & G. Rudebeck, eds.). 1:152–262. Almqvist & Wiksells, Uppsala.

Lourenço, W.R. 1985. Essai d'Interprétation de la Distribution du Genre *Opisthacanthus* (Arachnida, Scorpiones, Ischnuridae) dans les Régions Néotropicales et Afrotropicale. Étude Taxinomique, Biogéographique, Évolutive et Écologique. Thése de Doctorat d'État, Université Paris VI. 287 pp.

Lourenço, W.R. 1989. Rétablissement de la famille des Ischnuridae, distincte des Scorpionidae Pocock, 1893, à partir de la sous-famille des Ischnurinae Pocock, 1893. Revue Arachnologique 8:159–177.

Lourenço, W.R. 1996. Faune de Madagascar. 87. Scorpions (Chelicerata, Scorpiones). Muséum National d'Histoire Naturelle, Paris. 102 pp.

Lourenço, W.R. 1999. Considérations taxonomiques sur le genre *Hadogenes* Kraepelin, 1894; création de la sous-famille des Hadogeninae n. subfam., et description d'une espèce nouvelle pour l'Angola (Scorpiones, Scorpionidae, Hadogeninae). Revue Suisse de Zoologie 106:929–938.

Lourenço, W.R. 2000. Panbiogéographie, les familles des scorpions et leur répartition géographique. Biogeographica 76:21–39.

Newlands, G. 1972a. Ecological adaptations of Kruger National Park scorpionids (Arachnida: Scorpiones). Koedoe 15:37–48.

Newlands, G. 1972b. A description of *Hadogenes lawrencei* sp. nov. (Scorpiones) with a checklist and key to the South West African species of the genus *Hadogenes*. Madoqua 1:133–140.

Newlands, G. 1978. Arachnida (except Acari). Pp. 677–684. *In* Biogeography and Ecology of Southern Africa. (M.J.A. Werger, ed.). W. Junk, The Hague.

Newlands, G. 1980. A Revision of the Scorpion Genus *Hadogenes* Kraepelin 1894 (Arachnida: Scorpionidae) with a Checklist and Key to the Species. Unpubl. M.Sc. thesis. Potchefstroom University for C.H.E., Potchefstroom. 189 pp.

Newlands, G. & A.C. Cantrell. 1985. A re-appraisal of the rock scorpions (Scorpionidae: *Hadogenes*). Koedoe 28:35–45.

Newlands, G. & L. Prendini. 1997. Redescription of *Hadogenes zumpti* Newlands & Cantrell 1985: An unusual rock scorpion (Scorpiones, Ischnuridae) from the Richtersveld, South Africa. South African Journal of Zoology 32:76–81.

Paterson, H.E.H. 1991. The recognition of cryptic species among economically important insects. Pp. 1–10. *In Helionthis*: Research Methods and Prospects. (M.P. Zalucki, ed.). Springer-Verlag, New York.

Prendini, L. 1995. Patterns of Scorpion Distribution in Southern Africa: A GIS approach. Unpubl. B.Sc. (Hons.) thesis. University of Cape Town. 40 pp.

Prendini, L. 2000. Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): An exemplar approach. Cladistics 16:1–78.

Purcell, W.F. 1899. New South African scorpions in the collection of the South African Museum. Annals of the South African Museum 1:433–438.

Sissom, W.D. 1990. Systematics, biogeography and paleontology. Pp. 64–160. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford Univ. Press, Stanford, California.

Smithe, F.B. 1974. Naturalist's Color Guide Supplement. American Museum of Natural History, New York. 229 pp.

Smithe, F.B. 1975. Naturalist's Color Guide. American Museum of Natural History, New York, unpaginated.

Smithe, F.B. 1981. Naturalist's Color Guide. Part III. American Museum of Natural History, New York. 37 pp.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. Entomological News 81:297–316.

Vachon, M. 1973 (1974). Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. Bulletin du Muséum National d'Histoire Naturelle, Paris (3)140:857–958.

Van Rooyen, N. & G.J. Bredenkamp. 1996a. Mixed bushveld. P. 26. *In* Vegetation of South Africa, Lesotho and Swaziland. (A.B. Low & A.G. Rebelo, eds.). Dept. Environmental Affairs & Tourism, Pretoria.

Van Rooyen, N. & G.J. Bredenkamp. 1996b. Sour lowveld bushveld. Pp. 28–29. *In* Vegetation of South Africa, Lesotho and Swaziland. (A.B. Low & A.G. Rebelo, eds.). Dept. Environmental Affairs & Tourism, Pretoria.

Williams, S.C. 1971. Birth behavior in the South African scorpion *Hadogenes*. Pan-Pacific Entomologist 47:79–80.

FURTHER ADDITIONS TO THE SCORPION FAUNA
OF TRINIDAD AND TOBAGO

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ABSTRACT. The results of a study of new scorpion material, comprising nine species collected during a recent field trip to Trinidad and Tobago, are presented. The Trinidad population of *Tityus discrepans* (Karsch 1879) is described as a new species, *Tityus tenuicauda*, endemic to Trinidad, and more closely related to *Tityus arellanoparrai* González-Sponga 1985 than *T. discrepans*, both from Venezuela. A key to the identification of the three species is provided. New records are provided for *Ananteris cussinii* Borelli 1910, *Microtityus rickyi* Kjellesvig-Waering 1966, *Tityus clathratus* C.L. Koch 1844 and *Tityus melanostictus* Pocock 1893. Specimens of *Microtityus* collected on Tobago provide evidence for the synonymy of *Microtityus starri* Lourenço & Huber 1999 with *M. rickyi*. Previously unreported ecological observations are presented, including the burrowing biology of *Broteochactas laui* Kjellesvig-Waering 1966, and the microhabitat of *Chactas raymondhansorum* Francke & Boos 1986, which is apparently not restricted to water-filled spaces between the leaf sheaths of bromeliads.

Keywords: Scorpiones, Trinidad and Tobago, *Tityus*, *Microtityus*

Kjellesvig-Waering (1966) provided the first synopsis of the scorpion fauna of Trinidad and Tobago, wherein he recognized eight species in two families, Buthidae and Chactidae, and described a new buthid genus and species, *Microtityus rickyi* Kjellesvig-Waering 1966, and a new chactid species, *Broteochactas laui* Kjellesvig-Waering 1966. Francke & Boos (1986) subsequently revised the chactid scorpions of the islands, and described another new species, *Chactas raymondhansi* Francke & Boos 1986, from Trinidad. Sissom (2000) changed this name to *Chactas raymondhansorum* Francke & Boos 1986, in accordance with Article 31(a)(ii) of the International Code of Zoological Nomenclature (1985), since it is named after two people (Raymond A. Mendez and Hans Boos).

Recently, Lourenço & Huber (1999) published additional records of scorpions from Trinidad and Tobago, based on a large series of new material. These authors described another new buthid, *Microtityus starri* Lourenço & Huber 1999, and provided a brief account of the taxonomic status and geographical distribution of six of the other nine species known from Trinidad and Tobago: *Ananteris cussinii* Borelli 1910; *M. rickyi*; *Tityus discrepans* (Karsch 1879); *Tityus melanostictus* Pocock 1893; *Tityus trinitatis* Pocock 1897; *Broteochactas nitidus* Pocock 1893.

The author conducted a collecting trip to Trinidad and Tobago during July 1999 for the purpose of acquiring tissue samples and voucher specimens of Neotropical scorpions for DNA isolation and sequencing. This yielded 163 specimens, classified into nine species, from several localities, some of which are new records. The findings of this trip are reported here. New records are provided for *A. cussinii*, *M. rickyi*, *Tityus clathratus* C.L. Koch 1844 and *T. melanostictus*. Specimens of *Microtityus* collected on Tobago provide evidence for the synonymy of *M. starri* with *M. rickyi*. In addition, previously unreported ecological observations are presented, including the burrowing biology of *B. laui* and the microhabitat of the "bromeliad-dwelling scorpion" (Francke & Boos 1986; Rudd 1996; Ward 1996), *C. raymondhansorum*, which was recollected on Mt. El Tucuche.

The main finding presented here is the observation that the Trinidad population of *T. discrepans* is an undescribed species, quite distinct morphologically (and genetically) from the typical Venezuelan population. This new species, endemic to Trinidad, is described as *Tityus tenuicauda*. It is most closely related to *Tityus arellanoparrai* González-Sponga 1985, which is endemic to the highlands of northeastern Venezuela (González-Sponga

1985, 1996). A key, modified from González-Sponga (1996: 140), is provided for the identification of *T. arellanoparrai*, *T. discrepans* and *T. tenuicauda*.

Nine species are now recorded from Trinidad and Tobago, six of which are apparently endemic to the islands (Table 1). As noted by Francke & Boos (1986), the high percentage of scorpion endemism (67%) in Trinidad and Tobago supports Kjellesvig-Waering's (1966) hypothesis of speciation after faulting and subsequent erosion had isolated the islands from the South American mainland.

METHODS

Except where noted, all specimens listed were collected at night with the use of a portable ultraviolet light, comprising two mercury-vapor tubes attached to a chromium parabolic reflector and powered by a rechargeable 7 Amp/h, 12 V battery. A few others were collected during the day by turning stones, logs, tree bark, and inspecting other potential diurnal retreats. UV detection is known to greatly increase collecting yields and has led to the discovery of numerous undescribed species, even in previously well-collected areas (Lamoral 1979; Williams 1980; Sissom et al. 1990). Many scorpions, especially fossorial and humicolous forest species, cannot be collected with normal daytime collecting techniques.

All specimens examined (including the type specimens of *T. tenuicauda*) are deposited in the collection of the American Museum of Natural History, New York. Tissue samples of each species, stored in absolute ethanol, have been retained separately for DNA isolation and sequencing in the Ambrose Monell Collection for Molecular and Microbial Research at the American Museum of Natural History.   Illustrations of *T. discrepans* and *T. tenuicauda* were produced using a stereomicroscope and camera lucida. Measurements were made with digital calipers. Color designation follows Smithe (1974, 1975, 1981), trichobothrial notation follows Vachon (1974), and mensuration follows Stahnke (1970) and Lamoral (1979). Morphological terminology follows Couzijn (1976) for the segmentation of legs, Hjelle (1990) and Sissom (1990) for the segmentation of pedipalps, and Stahnke (1970), Lamoral (1979), and Sissom (1990) for other features. However, the terms used by previous authors (Stahnke 1970; Lamoral 1979; Sissom 1990) for certain metasomal carinae have been replaced with terms deemed more consistent and implying specific homology between carinae on segment V and those on the preceding segments. The term "ventral" (segments I–V) is replaced with "ventrosubmedian" (segment I only) and "ventromedian" (segments II–V only), and the term "dorsal" (segments I–IV only) is replaced with "dorsosubmedian."

KEY

Key to the identification of *Tityus arellanoparrai* González-Sponga 1985, *Tityus discrepans* (Karsch 1879) and **Tityus tenuicauda** new species (modified from González-Sponga 1996: 140), all of which are characterized by the presence of a single ventromedian carina on metasomal segments II–IV.

1. Chela manus of adult ♂ bulbous (Fig. 1), of adult ♀ slender (Fig. 2), with 15–16 rows of denticles on movable finger; metasomal segments of adult ♂ and ♀ short and stout, with large conical spiniform granules on dorsosubmedian carinae of segments II-IV and dorsolateral carinae of segment V (Figs. 5, 6); telson globose in ♂ and ♀ (Figs. 5, 6) . . . . *Tityus discrepans*
   Chela manus of adult ♂ and ♀ slender (Figs. 3, 4), with 14 rows of denticles on movable finger; metasomal segments of adult ♂ elongate and narrow (Fig. 7), of adult ♀ short and narrow (Fig. 8), with weakly developed rounded spiniform granules on dorsosubmedian carinae of segments II-IV and dorsolateral carinae of segment V (Figs. 7, 8); telson moderately globose in ♀, subadults and juveniles (Fig. 8), but distinctly elongated in adult ♂ (Fig. 7). 2
2. Metasomal segments I-II with lateral carinae obsolete; endemic to Venezuela . . . .
   . . . . *Tityus arellanoparrai*
   Metasomal segment I with lateral carinae fully developed, segment II with lateral carinae reduced to a few granules in distal third; endemic to Trinidad . . . . **Tityus tenuicauda**

Table 1.—Scorpion species recorded from Trinidad and Tobago. All except three are endemic to the islands. Species indicated with an asterisk have also been recorded from northern South America.

Family	Species	Trinidad	Tobago
Buthidae:	Ananteris cussinii*	x	x
	Microtityus rickyi	x	x
	Tityus clathratus*	x	
	Tityus tenuicauda	x	
	Tityus melanostictus*	x	
	Tityus trinitatis	x	x
Chactidae:	Broteochactas laui		x
	Broteochactas nitidus	x	x
	Chactas raymondhansorum	x	

FAMILY BUTHIDAE

Ananteris cussinii Borelli 1910

Ananteris cussinii Borelli 1910: 1–3.
Ananteris cussinii: Mello-Leitão 1932: 28; Hummelinck 1940: 144, 145, figs. 19, 20; Roewer 1943: 218; Mello-Leitão 1945: 243, 247, 248; Scorza 1954a: 159; Scorza 1954b: 189, 200; Kjellesvig-Waering 1966: 125, 128; Bücherl 1969: 767; González-Sponga 1971: 6–14, pl. 1–8; Vachon 1977: 298, figs. 10–14; Lourenço 1982: 138, 145, 146, figs. 31, 32, 44, 101; González-Sponga 1984: 61, 62, fig.; Armas 1988: 43, 44, 92, figs. 15, 16; Flórez 1991: 118; Lourenço 1993: 698, fig. 7; Rudloff 1994: 8; González-Sponga 1996: 118, 120, 121, figs. 276–278; Kovařík 1998: 103; Lourenço & Huber 1999: 250, 251; Fet & Lowe 2000: 61.
Ananteris cussini: Scorza 1954c: 165; Caporiacco 1951: 4; Esquivel de Verde & Machado-Allison 1969: 28; Armas 1977: 3; Cekalovic 1983: 189.
Ananteris cusinii: González-Sponga 1971: 9.

This species was reviewed by Kjellesvig-Waering (1966), Lourenço (1982), González-Sponga (1996), and Lourenço & Huber (1999). It occurs on the South American mainland (recorded from Colombia and Venezuela) and on Trinidad, but has not previously been reported from Tobago or from Gaspar Grande Island, off the northwestern peninsula of Trinidad. It was found in sympatry with *M. rickyi*, *T. trinitatis* and *B. laui* at Speyside, with *M. rickyi*, *T. clathratus* and *T. melanostictus* on Gaspar Grande, and with *M. rickyi*, *T. trinitatis* and *B. nitidus* at Mt. St. Benedict. All specimens personally collected were found running on open, stony ground in exposed areas (near paths and forest margins).

Material examined.—TRINIDAD AND TOBAGO: *Trinidad:* 1♂, Mt. St. Benedict, 10°39′49″N, 61°23′56″W, 30 June 1999, R. Pinto-da-Rocha; 1♂, Mt. St. Benedict, 9 July 1999, L. Prendini & I. Samad; 4♂2♀, Gaspar Grande Island, 7 July 1999, L. Prendini, H. Guarisco & I. Samad. *Tobago:* 2♂, Speyside, 1 km N on road to Charlotteville, 11°18′20″N, 60°32′15″W, 4 July 1999, L. Prendini & H. Guarisco.

Microtityus rickyi Kjellesvig-Waering 1966

Microtityus rickyi Kjellesvig-Waering 1966: 125, 131–134, figs. 3–8.
Microtityus starri Lourenço & Huber 1999: 253–259, figs. 11–22 (new synonym).
Microtityus rickyi: Vachon 1977: 285, 286, figs. 1–8; Lourenço & Eickstedt 1983: 71; Santiago-Blay 1985: 2; Lourenço 1986a: 232, fig. 1; Lourenço 1986b: 561, fig. 1; Armas 1988: 66; Santiago-Blay et al. 1990: 117; Kovarik 1998: 115; Lourenço & Huber 1999: 250, 252, 253; Fet & Lowe 2000: 184.
Microtityus ricky: Armas 1988: 93; Rudloff 1994: 8; Lourenço & Huber 1999: 256, tab. I.
Microtityus (Microtityus) rickyi: Armas 1974: 3.

Microtityus rickyi, previously considered endemic to Trinidad and the islands off its northwestern peninsula, was reviewed by Vachon (1977) and Lourenço & Huber (1999). Lourenço & Huber (1999) described *M. starri*, a new species from Little Tobago, an island just off the northeast coast of Tobago, but did not record that species, or *M. rickyi*, from Tobago itself.

The author collected several specimens of *Microtityus* from Speyside, on Tobago directly opposite Little Tobago. These specimens of *Microtityus*, the first to be collected from Tobago, demonstrate that *M. starri* should be regarded as a junior synonym of *M. rickyi*, and extend the range of that species to Tobago and adjacent islands.
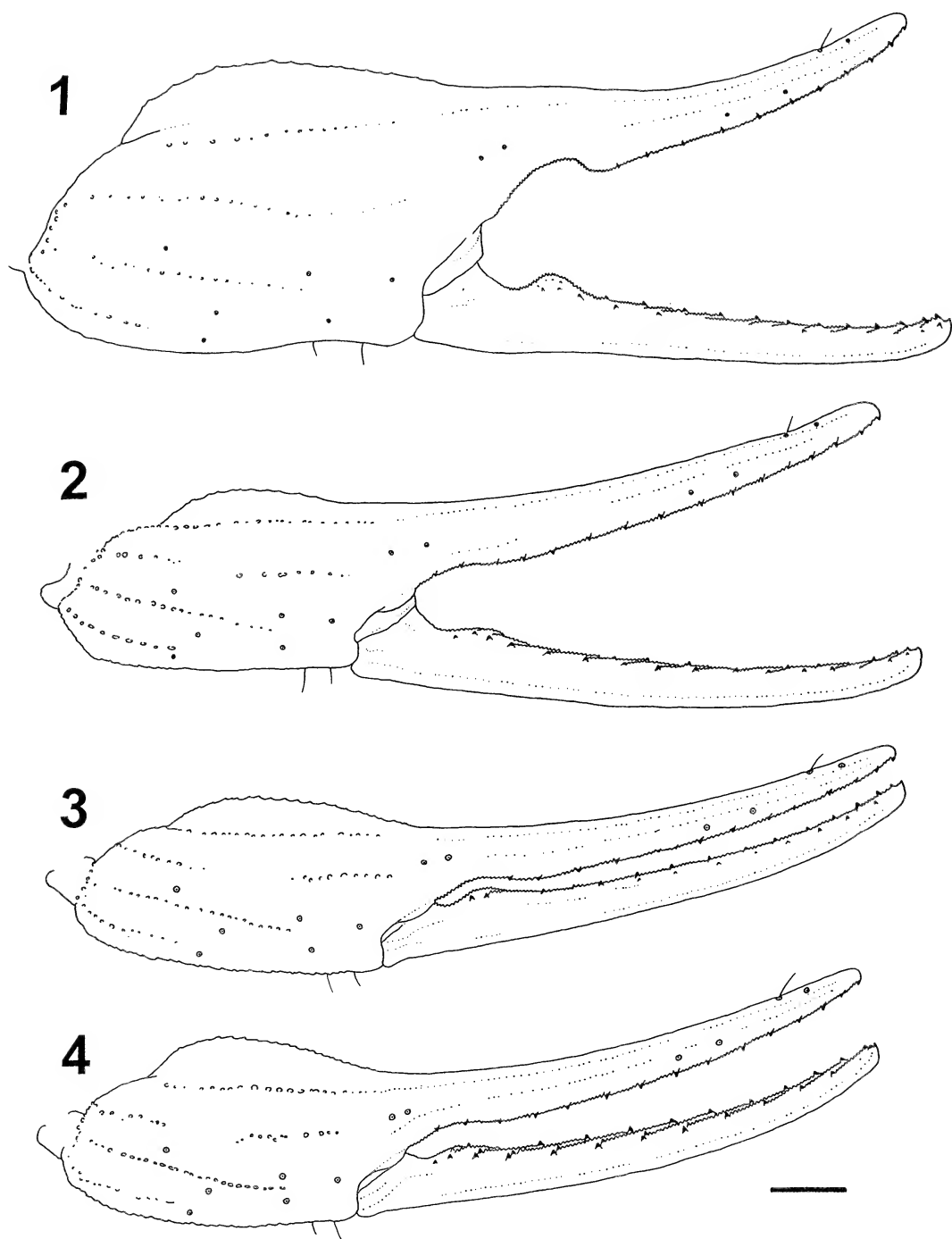
Figures 1–4.—External aspect of dextral pedipalp chelae from adult ♂ and ♀ *Tityus discrepans* (Karsch 1879) and ***Tityus tenuicauda*** new species, showing trichobothria, carinae and general shape. Scale bar = 1 mm. 1. *T. discrepans:* ♂ (AMNH), Venezuela, Edo. Miranda, 3 km E of Oraira, 400 m, 20 October 1969, M.A. González-Sponga; 2. *Tityus discrepans:* ♀ (AMNH), same data; 3. *Tityus tenuicauda:* paratype ♂ (AMNH), Trinidad, Chancellor Hill, Port of Spain, 1500 ft, August 1966, E.N. Kjellesvig-Waering; 4. *Tityus tenuicauda:* paratype ♀ (AMNH), Trinidad, 4 Fourth Street, Saddle Road, Maraval, 3 April 1957, T.H.G. Aitken.

According to Lourenço & Huber (1999), *M. starri* and *M. rickyi* can be reliably separated by examination of the trichobothria of the pedipalp femur. The trichobothrial pattern of *M. starri* is orthobothriotaxic, with d_2 present on the internal surface of the femur, whereas the pattern of *M. rickyi* is neobothriotaxic, with d_2 absent (Vachon 1977). In addition, the coloration of *M. starri* is darker overall, with metasomal segments IV, V and telson darker than segments I-III, and the pectinal tooth count is slightly lower (Lourenço & Huber 1999).

The latter differences in color and pectinal tooth count are well within the normal range of geographic variation for a given scorpion species—e.g., see Lourenço & Huber's (1999: 264) table III, showing pectinal tooth count variation in *T. trinitatis* from Trinidad and Tobago. These differences cannot, alone, provide species status for *M. starri*. Accordingly, recognition of *M. starri* as distinct from *M. rickyi* rests on the consistent presence of d_2, a tiny trichobothrium that is reduced or lost in a number of apparently unrelated buthids. However, in some of the newly collected Speyside specimens, an atrophied trichobothrium is evident in the position of d_2, while this trichobothrium is absent in other specimens from the same locality. The observation that the presence or absence of d_2 is polymorphic in the Speyside population casts doubt on the utility of this character for the separation of *Microtityus* species and provides my rationale for the synonymy of *M. starri* with *M. rickyi*.

Microtityus rickyi was found in sympatry with *A. cussinii*, *T. clathratus* and *T. melanostictus* at Gaspar Grande, with *A. cussinii*, *T. trinitatis* and *B. nitidus* at Mt. St. Benedict, and with *A. cussinii*, *T. trinitatis* and *B. laui* at Speyside. All specimens were found motionless on rocks, tree trunks or bare soil banks, often with only the carapace and pedipalps protruding from holes or crevices in the substratum. Specimens were observed from ground level to several meters up tree trunks.

Material examined.—TRINIDAD AND TOBAGO: *Trinidad:* 11♂17♀, Mt. St. Benedict, 10°39′49″N, 61°23′56″W, 28 June 1999, L. Prendini; 4♀, Mt. St. Benedict, 9 July 1999, L. Prendini & I. Samad; 4♂9♀, Gaspar Grande Island, 7 July 1999, L. Prendini, H. Guarisco & I. Samad. *Tobago:* 13♂27♀, Speyside, 1 km N on road to Char-

lotteville, 11°18′20″N, 60°32′15″W, 3–4 July 1999, L. Prendini & H. Guarisco.

Tityus clathratus C.L. Koch 1844

Tityus clathratus C.L. Koch 1844: 22–24, pl. CCCLXVI, fig. 861.
Tityus quelchii Pocock 1893a: 314, 315, pl. XIV, fig. 1 (synonymized by Kraepelin 1899: 85).
Tityus fahrenholtzi Roewer 1943: 223, 224, figs. 6, 6a-e (synonymized by Lourenço 1984a: 357).
Tityus guianensis Caporiacco 1947: 20 (synonymized by Lourenço 1984a: 352).
Tityus clathratus: C.L. Koch 1850: 91; Kraepelin 1899: 75, 85, 86; Kraepelin 1901: 269; Kraepelin 1908: 187, 190, 193, 194; Mello-Leitão 1931: 119, 141; Mello-Leitão 1932: 29; Mello-Leitão 1939: 58, 64, 67; Roewer 1943: 224; Mello-Leitão 1945: 299, 304, 320–322, figs. 129, 130; Waterman 1950: 168; Caporiacco 1951: 4; Scorza 1954a: 161; Scorza 1954b: 191, 201, fig. 20; Scorza 1954c: 166; Bücherl 1967: 111; Bücherl 1969: 767; Esquivel de Verde 1969: 217, 218, fig. 5; Esquivel de Verde & Machado-Allison 1969: 34; Bücherl 1971: 327; Bücherl 1978: 372; González-Sponga 1978: 197, 201, figs. 9, 273, 274; Cekalovic 1983: 190; Lourenço 1983: 777, figs. 19–25, 118; Lourenço 1984a: 350, 352, figs. 1–3, 15–18, tab. I, II; Brignoli 1985: 415; Lourenço 1986a: 232, fig. 2; Lourenço 1986b: 562, fig. 2; Armas 1988: 74, 75, 93; Lourenço 1991: 116; Lourenço 1992: 476, fig. 5, tab. I; Rudloff 1994: 9; González-Sponga 1996: 118, 154, figs. 357–359; Lourenço 1997: 591; Kovařík 1998: 120; Fet & Lowe 2000: 238, 239.
Tityus quelchii: Kraepelin 1895: 92; Pocock 1897a: 363; Pocock 1897b: 520; Kjellesvig-Waering 1966: 125, 129.
Tityus guianensis: Caporiacco 1948: 610, 611, figs. 4, 5.
Tityus quelchi: Lourenço 1984a: 352, tab. I.

This species was reviewed by Kjellesvig-Waering (1966), Lourenço (1984a) and González-Sponga (1996). It is evidently widespread in South America east of the Andes (recorded from Brazil, French Guiana, Guyana, Suriname, Venezuela and Trinidad), but has not previously been reported from the islands between the northwestern peninsula of Trinidad and the Paria Peninsula of Venezuela. It was found in sympatry with *A. cussinii*, *M. rickyi* and *T. melanostictus* at Gaspar Grande. All specimens were found motionless on bare soil banks or leaf litter in exposed areas (near paths and forest margins). No specimens were collected above ground level (cf. *T. melanostictus*).

Material examined.—TRINIDAD AND TO-BAGO: *Trinidad:* 8♀, Gaspar Grande Island, 7 July 1999, L. Prendini, H. Guarisco & I. Samad.

Tityus melanostictus Pocock 1893

Tityus melanostictus Pocock 1893b: 377, 381, 382, pl. XXIX, figs. 4, 4b.

Tityus melanostictus: Kraepelin 1895: 92; Kraepelin 1899: 74, 84; Kraepelin 1901: 269; Kraepelin 1908: 190, 193; Mello-Leitão 1931: 120, 141; Mello-Leitão 1939: 60, 64, 72; Werner 1939: 352; Mello-Leitão 1945: 300, 309, 339–341, figs. 2, 137–139; Caporiacco 1951: 40; Scorza 1954a: 162; Scorza 1954b: 191, 202; Scorza 1954c: 166; Weidner 1959: 104; Kjellesvig-Waering 1966: 125, 128, 129; Esquivel de Verde 1969: 220, fig. 7; Esquivel de Verde & Machado-Allison 1969: 28; Bücherl 1971: 327; Bücherl 1978: 372; Lourenço 1984a: 354, 355, figs. 7–18, tables I, II; Lourenço 1986a: 232, fig. 3; Lourenço 1986b: 562, fig. 15; Lourenço & Eickstedt 1987: 89, 90, tab. I; Armas 1988: 78, 79, 93; González-Sponga 1989: 218; Rudloff 1994a: 9; González-Sponga 1996: 118, 155, figs. 360–362; Kovařík 1998: 121; Lourenço & Huber 1999: 259, 260; Fet & Lowe 2000: 250.

Tityus melanosticus: Waterman 1950: 168.

Tityus melanostrihus: Cekalovic 1983b: 190.

This species was reviewed by Kjellesvig-Waering (1966), Lourenço (1984a), Lourenço & Eickstedt (1987), González-Sponga (1996) and Lourenço & Huber (1999). It occurs on the South American mainland (Venezuela), on Trinidad, Tobago, and the islands between the northwestern peninsula of Trinidad and the Paria Peninsula of Venezuela. It was found in sympatry with *A. cussinii*, *M. rickyi* and *T. clathratus* at Gaspar Grande. All specimens were found motionless on tree branches, at least 1 m above ground level, indicating that this is an arboreal species (cf. *T. clathratus*).

Material examined.—TRINIDAD AND TO-BAGO: *Trinidad:* 2♂1♀, Gaspar Grande, 7 July 1999, L. Prendini, H. Guarisco & I. Samad.

Tityus tenuicauda new species
Figs. 3, 4, 7, 8; Table 2

Tityus discrepans (misidentification): Kjellesvig-Waering 1966: 128; Kovařík 1998: 120 (part); Lourenço & Huber 1999: 259; Fet & Lowe 2000: 242, 243 (part).

Tityus discrepans was described from Caracas, Venezuela, but has also been reported from Brazil, Guyana and Suriname (Fet &

Lowe 2000). Kjellesvig-Waering (1966: 128) reported the first records of *T. discrepans* from Trinidad, noting that the "Trinidad form differs slightly from those in Venezuela and Guyana . . . as both the male and female have well developed lobes on the free finger of the pedipalp [and the] number of rows of denticles almost always is 15, as against 16."

Lourenço (1982) later described *Tityus gasci* Lourenço 1982 from French Guiana, which he maintained was most closely related to *T. discrepans*, while González-Sponga (1981) described *Tityus pittieri* González-Sponga 1981, and subsequently (González-Sponga 1985) *T. arellanoparrai*, two closely related species from Venezuela. González-Sponga (1996) provided a detailed key to the identification of *T. arellanoparrai*, *T. discrepans*, and *T. pittieri*. Recently, Lourenço & Huber (1999: 259) provided additional records of *T. discrepans* from Trinidad, but noted that the species "remains poorly known."

As part of a separate study investigating scorpion higher phylogeny, a tissue sample of *T. discrepans* was obtained from the type locality, Caracas, for DNA isolation and sequencing. When the resultant sequences were compared with sequences of homologous gene regions obtained from tissue samples of *T. discrepans* and *T. trinitatis* from Trinidad, greater percentage similarity was observed between the latter two samples than between the samples of *T. discrepans* from Venezuela and Trinidad. On closer inspection of *T. discrepans* specimens from Venezuela and Trinidad in the collection of the AMNH, it became clear that the Trinidad population is not conspecific with *T. discrepans*, but constitutes an undescribed species, differing quite considerably from the latter in external morphology. It is here described as *Tityus tenuicauda*.

Types.—TRINIDAD AND TOBAGO: *Trinidad:* Holotype ♀, Trinidad Regional Virus Lab. Building, Wrightson Road, Port of Spain, 14 March 1955, T.H.G. Aitken. Paratypes: 1♂, 1 juv ♀ [DNA sample], Mt. El Tucuche (summit), 8 July 1999, L. Prendini & I. Samad; 1♂, 1 juv ♂, 1 juv ♀, Chancellor Hill, Port of Spain, 1500 ft, August 1966, E.N. Kjellesvig-Waering; 1♀, 4 Fourth Street, Saddle Road, Maraval, 3 April 1957, T.H.G. Aitken.

Etymology.—The specific name refers to the long, slender metasoma of the adult male.

Relationships.—*Tityus tenuicauda* occurs in the *discrepans* group of *Tityus*, which also includes *T. arellanoparrai*, *T. discrepans* and *T. pittieri*, all of which are characterized by the presence of a single ventromedian carina on metasomal segments II-IV (González-Sponga 1996). This unusual character is hypothesized to be synapomorphic for these species, as most other species of *Tityus* display paired ventrosubmedian carinae on these segments (although, in certain species, these may be partially fused into a single ventromedian carina on some segments).

Although the hypothesis that a single ventromedian carina on metasomal segments II-IV is synapomorphic for the *discrepans* group remains to be tested cladistically, the available evidence refutes Lourenço's (1982) claim that *T. discrepans* is the closest relative of *T. gasci*. *Tityus gasci* displays paired ventrosubmedian carinae on segments I-IV (the hypothesized plesiomorphic condition for *Tityus*), and no other potential synapomorphies were provided for the two species by Lourenço (1982): "A notre avis, la seule espèce qui se rapproche de *Tityus gasci* est *Tityus discrepans* (Karsch, 1879) qui a été signalée en Guyane française par Mello-Leitão, en 1945. Elles peuvent néanmoins être distinguées l'une de l'autre par la disposition des carènes ventrales du metasoma: chez *Tityus gasci* ces carènes cv (fig. 10 [illustrating paired ventrosubmedian carinae on metasomal segments I-IV]) sont paires dans les anneux I à IV, alors que chez *Tityus discrepans* il n'existe qu'une seule carène ventrale axiale, cva (fig. 11 [illustrating paired ventrosubmedian carinae on metasomal segment I, and a single ventromedian carina on segments II-IV])."

Diagnosis.—The presence of a single ventromedian carina on metasomal segments II-IV serves to distinguish *T. tenuicauda* from all other *Tityus* species in Trinidad (Kjellesvig-Waering 1966; Lourenço & Huber 1999). Although it has been referred to *T. discrepans*, *T. tenuicauda* is actually more closely related to another member of the *discrepans* group, *T. arellanoparrai*, from the highlands of northeast Venezuela (González-Sponga 1985, 1996).

Both species are readily separated from *T. discrepans* by the slender pedipalp chelae (Fig. 3) and slender, elongated metasomal segments (Fig. 7) of the adult ♂; in adult ♂ *T.*

discrepans, the chelae are bulbous (Fig. 1) and the metasomal segments are short and stout (Fig. 5). *Tityus discrepans* can be further distinguished by the presence of large conical spiniform granules on the dorsosubmedian carinae of metasomal segments II-IV and dorsolateral carinae of segment V (Figs. 5, 6); in *T. arellanoparrai* and *T. tenuicauda*, the spiniform granules are small and rounded, especially on segment V (Figs. 7, 8). Finally, *T. discrepans* can be distinguished by the greater number of rows of denticles on the movable finger of the pedipalp chela (Table 2; note that the counts reported by Kjellesvig-Waering [1966] and González-Sponga [1996] included the apical row).

Tityus tenuicauda can be readily separated from *T. arellanoparrai* by the presence of fully developed median lateral carinae of metasomal segment I; in *T. arellanoparrai* the median lateral carinae of segment I are obsolete.

Description.—The following description is based primarily on the holotype ♀ and a paratype ♂ (Chancellor Hill).

Color: Carapace, tergites, metasomal segments I-IV, pedipalps, and dorsal surfaces of legs: Maroon No. 31. Metasomal segment V, telson and chela fingers: Warm Sepia No. 221A. Chelicerae, sternites, and ventral surfaces of legs: Cinnamon-Brown No. 33. Distal edges of post-tergites and post-sternites: Buff No. 124. Pectines and genital operculum: Cream Color No. 54. Metasomal segment V, telson and chela fingers distinctly infuscated, whereas distal edges of tergites and sternites distinctly lighter in color. Slight infuscation in interocular region of carapace.

Carapace: Carapace coarsely and sparsely granular, mainly on interocular and posterolateral surfaces. Anterior and posterior margins of carapace procurved. Three pairs of lateral ocelli. Median ocelli considerably larger than lateral ocelli, situated anteromedially. Ocular tubercle with pair of smooth superciliary carinae, protruding slightly above median ocelli. Superciliary carinae connected anteriorly to pair of granular anteromedian carinae, but disconnected from pair of granular posteromedian carinae. Weakly developed, granular carina extending posteriorly from proximal lateral ocellus on each side of carapace. Anteromedian furrow moderately deep, ovate; posteromedian furrow narrow, shallow anteriorly, deep posteriorly; posterolateral furrows

5

6

7

8
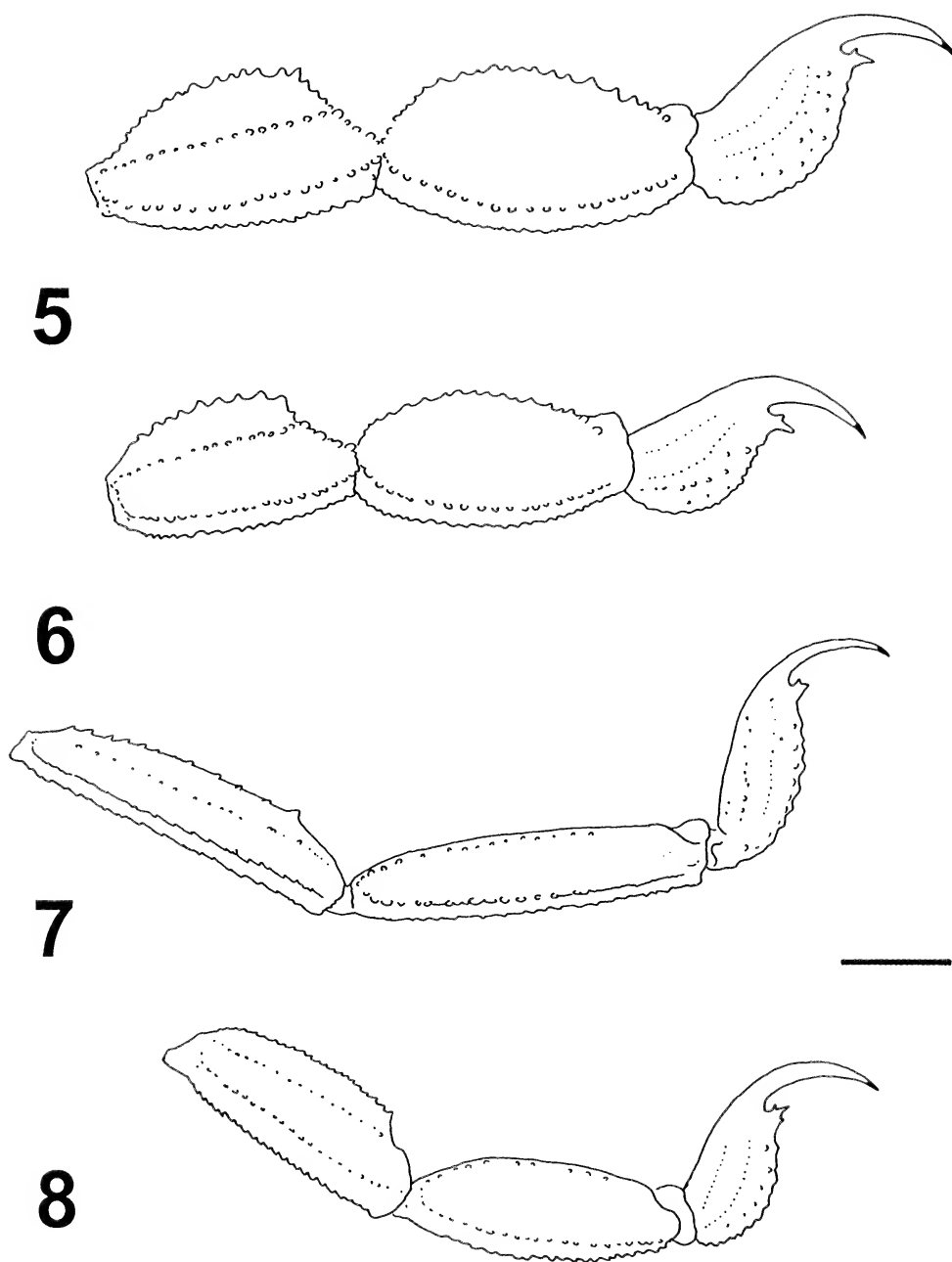
Figures 5–8.—External aspect of metasomal segments IV-V and telson from adult ♂ and ♀ *Tityus discrepans* (Karsch 1879) and **Tityus tenuicauda** new species, showing carinae, spiniform granules, and general shape. Scale bar = 3 mm. 5. *T. discrepans:* ♂ (AMNH), Venezuela, Edo. Miranda, 3 km E of Oraira, 400 m, 20 October 1969, M.A. González-Sponga; 6. *T. discrepans:* ♀ (AMNH), same data; 7. *Tityus tenuicauda:* paratype ♂ (AMNH), Trinidad, Chancellor Hill, Port of Spain, 1500 ft, August 1966, E.N. Kjellesvig-Waering; 8. *Tityus tenuicauda:* paratype ♀ (AMNH), Trinidad, 4 Fourth Street, Saddle Road, Maraval, 3 April 1957, T.H.G. Aitken.

shallow, wide, curved; posteromarginal furrow narrow, deep.

Chelicerae: Movable finger with distal external and distal internal teeth equal, apposable. Ventral aspect of fingers and manus with long, dense macrosetae.

Sternum: Subtriangular. Median longitudinal furrow Y-shaped, shallow anteriorly, deep and narrow posteriorly.

Pedipalps: Femur pentacarinate; carinae distinct, costate granular, with spiniform granules on internomedian carina; intercarinal surfaces finely and uniformly granular. Patella with seven distinct, costate granular carinae; intercarinal surfaces smooth; internomedian carina with several large spiniform granules proximally, becoming smaller distally; basal tubercle moderately developed. Chela with nine carinae; intercarinal surfaces smooth; dorsal and external carinae distinct, costate granular; internal carinae obsolete, weakly granular (♀) to smooth (♂). Digital carina distinct, costate granular, and discontinuous medially (Figs. 3, 4). External surface with short, costate granular accessory carina. Chela long and slender, length along ventroexternal carina 39% (♂) to 44% (♀) greater than chela width and 47% (♂) to 49% (♀) greater than chela height; length of movable finger 47% (♂) to 48% (♀) greater than length along ventroexternal carina. Chela with small proximal lobe on movable finger and shallow notch in fixed finger. Dentate margins of chela fingers with 13 oblique granular rows on fixed finger, each row terminating in a large granule at the proximal and distal ends, and with 14 rows on movable finger, plus a short apical row of four granules; supernumerary granules absent; chela fingers each with a terminal denticle.

Trichobothria: Orthobothriotaxic, type A, α configuration, with the following segment totals: femur 11 (5 dorsal, 4 internal, 2 external), patella 13 (5 dorsal, 1 internal, 7 external) and chela 15 (8 manus, 7 fixed finger). Total number of trichobothria per pedipalp, 39. Trichobothrium d_5 of pedipalp femur distinctly basal to e_1.

Mesosoma: Tergites entirely granular, finely on pretergites, coarsely on post-tergites, becoming more so distally; I-VII each with a strongly developed, granular median carina; VII additionally with distinct pairs of costate granular dorsosubmedian and dorsolateral carinae. Sternites smooth (♂) to finely granular

medially (♀); I-VII each with an obsolete, smooth median carina; VII additionally with paired, costate granular ventrosubmedian and ventrolateral carinae. Distal edge of sternite V with smooth projection medially.

Pectines: First proximal median lamella of each pecten slightly dilated in ♀. Pectinal teeth: 18/18 (♂), 17/19 (♀). The left pecten of the holotype is damaged, but the pectinal tooth count for the paratype ♀ from Maraval is 19/19.

Genital operculum: Completely divided longitudinally. Genital papillae present (♂), absent (♀).

Legs: Tibia III-IV without spurs. Basitarsi each with paired rows of fine macrosetae on retrolateral, and to a lesser extent, prolateral margins. Telotarsi each with paired ventrosubmedian rows of fine macrosetae. Telotarsal laterodistal lobes truncated; median dorsal lobes extending to ungues. Telotarsal ungues short, distinctly curved, and equal in length.

Metasoma and telson: Metasomal segments I-V progressively increasing in length, and decreasing in width, with segment V 19% narrower than segment I; width percentage of length 36% (♂) to 46% (♀) for I, 27% (♂) to 39% (♀) for II, 24% (♂) to 34% (♀) for III, 22% (♂) to 29% (♀) for IV, and 19% (♂) to 29% (♀) for V, giving the metasoma a slender appearance. Telson oval (Figs. 7, 8), height 38% (♂) to 45% (♀) of length, with flattened dorsal surface and rounded ventral surface; moderately globose in ♀, but distinctly elongated in ♂; vesicle not distinctly narrower than metasomal segment V, width 95% (♂) to 98% (♀) of metasomal segment V. Metasoma with intercarinal surfaces smooth, but with carinae granular to costate granular. Metasomal segments II-IV with distal granules of dorsosubmedian carinae enlarged, spiniform. Ten carinae on segment I, nine carinae on segment II, seven carinae on segments III-IV, and five carinae on segment V. Segment I with paired ventrosubmedian carinae; segments II-V with single ventromedian carina. Median lateral carinae fully developed on segment I, reduced to a few granules in the distal third of segment II, and absent in segments III-V. Segment V with paired dorsolateral and ventrolateral carinae. Telson with five obsolete granular carinae, and a well developed, spinoid subaculear tubercle, directed towards the base of the aculeus, and unevenly bifurcated distally

(Figs. 7, 8). Aculeus long, 56% (♂) to 66% (♀) of vesicle length, and sharply curved.

Hemispermatophore: Flagelliform.

Geographic variation: The paratype ♂ from Mt. El Tucuche has a higher pectinal tooth count (19/19) than the paratype ♂ from Chancellor Hill.

Ontogenetic variation: As in other species of *Tityus,* ♂ resembles ♀ very closely until the final instar. However, juveniles and sub-adults can be readily sexed by examination of the pectines and genital aperture.

Sexual dimorphism: In addition to above-mentioned characters, adult ♂ are slightly longer than adult ♀. The increased length of ♂ is attributed mainly to the longer metasomal segments: metasomal length approximately 69% of total length (♂); approximately 66% (♀). Adult ♂ are considerably more slender than adult ♀, with sternite VII length:width ratio 32% lower.

Measurements: As in Table 2.

Distribution.—*Tityus tenuicauda* is endemic to, and evidently widespread in Trinidad. In addition to the type localities at Port of Spain, Maraval, and Mt. El Tucuche, this species has been recorded from Petit Valley, Comuto, Sangre Grande, Bush-Bush Forest (Nariva Swamp), and Mayaro by Kjellesvig-Waering (1966), and from Mt. St. Benedict (Tunapuna) by Lourenço & Huber (1999).

Ecology.—As noted by Kjellesvig-Waering (1966), this species is uncommon, probably because it is arboreal and thus seldom collected. The only specimens personally collected, from cloud forest at the summit of Mt. El. Tucuche, were located with UV light sitting motionless on tree branches about 2 m above the ground. Kjellesvig-Waering (1966: 128) reported that this is "a forest species, and has been taken from trees as much as fifty feet [16 m] above ground." Ward (1996: 76) reported collecting three specimens of this species from bromeliads, *Glomeropitcairnia erectiflora,* on the summit of Mt. El Tucuche, but noted that it can also be found "under debris." *Tityus tenuicauda* was collected in sympatry with *B. nitidus* and *C. raymondhansorum* on the summit of Mt. El Tucuche.

Tityus trinitatis Pocock 1897

Tityus trinitatis Pocock 1897b: 514, 517, 518.
Isometrus androcottoides (misidentification): Pocock 1889: 57.

Tityus androcottoides (misidentification): Pocock 1893b: 377, 378, pl. XXIX, figs. 3, 3b (part).
Tityus trinitatis: Kraepelin 1899: 71, 78; Mello-Leitão 1931: 136, 147; Mello-Leitão 1939: 62, 65, 66; Mello-Leitão 1945: 302, 304, 432–434, figs. 176–182; Waterman 1950: 168, 171, fig.; Caporiacco 1951: 41; Scorza 1954a: 161; Scorza 1954b: 190, 207, figs. 22, 23; Scorza 1954c: 166; Scorza 1954d: 7, 8, fig.; Bücherl 1959: 259; Bücherl 1964: 59; Kjellesvig-Waering 1966: 125, 129, 130; Bücherl 1969: 768; Esquivel de Verde & Machado-Allison 1969: 35; Bücherl 1971: 327, 330, 332, fig. 4; González-Sponga 1974a: 58; Bücherl 1978: 372, 375; Lourenço 1984b: 15–19, figs. 1–10, tab. I; Kjellesvig-Waering 1986: 86, figs. 31C, D; Armas 1988: 82, 83, 93, figs. 31, 32A, 35; Rudloff 1994: 9; Lourenço 1995: 29; Kovařík 1998: 122; Lourenço & Huber 1999: 259, 261–263; Fet & Lowe 2000: 263, 264.

This species was reviewed by Kjellesvig-Waering (1966), Lourenço (1984b) and Lourenço & Huber (1999). It is endemic to Trinidad, Tobago, and the islands off the northwestern peninsula of Trinidad. The Venezuelan record of Scorza (1954b: 207) is presumably erroneous, and the species was omitted by González-Sponga (1996). *Tityus trinitatis* is the most common species of scorpion in Trinidad and Tobago, and has been collected in sympatry with *A. cussinii, M. rickyi* and *B. laui* at Speyside, and with *A. cussinii, M. rickyi* and *B. nitidus* at Mt. St. Benedict. Most specimens were found motionless on bare ground, leaf litter, rock faces, logs and branches close to ground level. Several adult specimens were observed preying on *M. rickyi,* and on juvenile conspecifics.

Material examined.—TRINIDAD AND TOBAGO: *Trinidad:* 1♂, Arima road, 10°42′22″N, 61°17′29″W, 29 June 1999, L. Prendini & R. Pinto-da-Rocha, in palm leaf base; 1 juv ♂, Arima, 8 km N, 29 July 1999, B. Cutler, in fern frond; 2♀, 2 juv, Mt. St. Benedict, 10°39′49″N, 61°23′56″W, 28 June 1999, L. Prendini; 1♀, 2 juv, Mt. St. Benedict, 9 July 1999, L. Prendini & I. Samad. *Tobago:* 2♂5♀, Speyside, 1 km N on road to Charlotteville, 11°18′20″N, 60°32′15″W, 3 July 1999, L. Prendini & H. Guarisco; 1♂4♀, 2 juv, same data, except 4 July 1999.

FAMILY CHACTIDAE

Broteochactas laui Kjellesvig-Waering 1966

Broteochactas laui Kjellesvig-Waering 1966: 125–128, figs. 1, 2.
Broteochactas laui: González-Sponga 1974b: 5;

Table 2.—Meristic data for adult ♂ and ♀ *Tityus discrepans* (Karsch 1879) and **Tityus tenuicauda** new species. *T. discrepans*: ♂, ♀ (AMNH), Venezuela, Edo. Miranda, 3 km E of Oraira, 400 m, 20 October 1969, M.A. González-Sponga. *Tityus tenuicauda*: holotype ♀ (AMNH), Trinidad, Trinidad Regional Virus Lab. Building, Wrightson Road, Port of Spain, 14 March 1955, T.H.G. Aitken; paratype ♂ (AMNH), Trinidad, Chancellor Hill, Port of Spain, 1500 ft, August 1966, E.N. Kjellesvig-Waering. Measurements following Stahnke (1970) and Lamoral (1979). [1] Total length = sum of carapace, tergites I-VII, metasomal segments I-V and telson. [2] Not including the apical row (Wagner 1977; Sissom & Lourenço 1987). [3] Left pecten of holotype ♀ damaged, count for paratype ♀ from Maraval (AMNH): 19/19.

| | | *T. discrepans* | | *T. tenuicauda* | |
		♂	♀	♂	♀
Total length[1]		77.81	67.36	80.30	73.85
Carapace	length	7.77	7.37	6.87	7.07
	anterior width	4.99	4.83	4.04	4.70
	posterior width	7.66	8.00	6.09	7.27
Mesosoma + telson	total length	21.85	18.63	17.98	18.09
Sternite VII	length	5.32	4.73	4.97	4.66
	width	6.94	7.66	4.96	6.86
Metasoma	total length	48.19	41.36	55.45	48.69
Metasomal segment I	length	6.36	5.22	7.19	6.99
	width	4.09	3.71	2.65	3.24
Metasomal segment II	length	7.65	6.36	8.78	7.64
	width	4.12	3.79	2.41	2.99
Metasomal segment III	length	8.01	6.87	9.86	8.24
	width	4.22	3.80	2.37	2.80
Metasomal segment IV	length	8.52	7.09	10.30	8.60
	width	4.38	3.81	2.30	2.51
Metasomal segment V	length	8.94	8.12	11.18	9.15
	width	4.44	3.86	2.15	2.61
Telson	total length	8.71	7.70	8.14	8.07
	aculeus length	3.53	2.85	3.29	3.57
	vesicle length	6.02	5.12	5.90	5.41
	vesicle width	3.84	3.16	2.11	2.47
	vesicle height	3.24	2.75	2.23	2.42
Pedipalp	total length	33.64	30.47	30.10	31.43
Femur	length	7.49	6.60	6.77	6.70
	width	2.16	2.09	1.78	2.04
Patella	length	7.69	7.07	7.28	7.46
	width	3.35	2.91	2.55	3.04
Chela	length	14.30	12.98	12.92	13.55
	width	4.26	2.74	2.46	2.85
	height	3.79	2.38	2.27	2.48
	length along ventroexternal carina	5.37	4.15	4.41	4.68
	length of movable finger	9.03	8.85	8.52	8.86
	rows of denticles fixed (left/right)	13/13	13/14	13/13	13/13
	rows of denticles mov.[2] (left/right)	15/15	15/15	14/14	14/14
Pecten	total length	4.71	4.31	4.61	4.90
	length along dentate margin	4.49	4.11	4.44	4.24
	tooth count (left/right)	16/16	17/17	18/18	17/19[3]

González-Sponga 1974c: 300; González-Sponga 1975: 49; Francke & Boos 1986: 24–27, figs. 21–26; Kovařík 1998: 125; Sissom 2000: 292, 293.

This species, which is endemic to Tobago, was reviewed by Francke & Boos (1986), but nothing was previously known of its biology. As a result of observations made on 14 specimens collected by the author, *B. laui* is now known to be a fossorial scorpion which constructs burrows, approximately 10 cm in length, into hard soil banks. The burrow en-

trances, situated in open ground, are oval in shape and approximately 10 mm wide. The burrows are constructed at an angle into the soil. Most of the specimens were located with UV detection, as their pedipalps were partially extended from their burrow entrances. On discovery, they immediately retreated backwards into their burrows and had to be excavated. One adult ♂ was located on the ground surface. *Broteochactas laui* was collected in sympatry with *A. cussinii*, *M. rickyi* and *T. trinitatis* at Speyside.

Material examined.—TRINIDAD AND TOBAGO: *Tobago:* 3♂12♀, Speyside, 1 km N on road to Charlotteville, 11°18′20″N, 60°32′15″W, 3–4 July 1999, L. Prendini & H. Guarisco.

Broteochactas nitidus Pocock 1893

Broteochactas nitidus Pocock 1893b: 399–401, pl. XXIX, figs. 7, 7a.
Broteochactas gollmeri (misidentification): Kraepelin 1894: 176, 177 (part); Pocock 1897a: 365, 366 (part); Kraepelin 1899: 173 (part); Pocock 1900: 68 (part); Kraepelin 1912: 53 (part?); Mello-Leitão 1932: 32 (part); Roewer 1943: 237; Mello-Leitão 1945: 100 (part); Waterman 1950: 169; Kjellesvig-Waering 1966: 125, 126, fig. 2.
Broteochactas nitidus: Francke & Boos 1986: 21–25, figs. 15–20; González-Sponga 1992: 54; Ward 1996: 10; Kovařík 1998: 125; Lourenço & Huber 1999: 263; Sissom 2000: 293.

This species, which is endemic to Trinidad and Tobago, was reviewed by Kjellesvig-Waering (1966) under the name *B. gollmeri* (Karsch 1879), with which it was confused. Francke & Boos (1986) reinstated the name, *B. nitidus*. The species was reviewed recently by Lourenço & Huber (1999). Like *B. laui*, *B. nitidus* is a fossorial scorpion which constructs burrows in hard soil. The burrows appear to be shorter than those of *B. laui* and are usually constructed under logs or stones (*n* = 6). One specimen was found inside a rotten log. However, six of the specimens were found motionless on bare ground at night. *Broteochactas nitidus* was found in sympatry with *A. cussinii*, *M. rickyi* and *T. trinitatis* at Mt. St. Benedict, and with *C. raymondhansorum* and *T. tenuicauda* on the summit of Mt. El Tucuche.

Material examined.—TRINIDAD AND TOBAGO: *Trinidad:* 7♀, 3 juv, Mt. St. Benedict, 10°39′49″N, 61°23′56″W, 28 June 1999, L. Prendini; 1♀, Arena Forest, 10°34′54″N, 61°14′20″W, 1

July 1999, L. Prendini, in rotten log; 1♀, Mt. Zion, 6 July 1999, L. Prendini & H. Guarisco, in burrow under stone; 1♂, Mt. El Tucuche (summit), 8 July 1999, L. Prendini & I. Samad.

Chactas raymondhansorum Francke & Boos 1986

Chactas (Andinochactas) raymondhansi Francke & Boos 1986: 16–19, figs. 1–10.
Chactas raymondhansi: Ward 1996: 10; Rudd 1996: 79–87.
Chactas ryamondhansi: Kovařík 1998: 126.
Chactas raymondhansorum: Sissom 2000: 305.

Chactas raymondhansorum, the largest scorpion in Trinidad, is known only from cloud forest at the summits of the highest mountains in the Northern Range: Cerro Del Aripo (990 m), Mt. El Tucuche (980 m) and Morne Bleu (800 m). In their original description, Francke & Boos (1986: 19) noted that all specimens had been collected from "water-filled spaces between leaf sheaths of the bromeliad *Glomeropitcairnia erectiflora* Mez." and proposed that the species was a bromeliad specialist, with "a large chamber extending from the stigmata and surrounding the book lungs . . . [that] may act as a reservoir for air if submersion becomes necessary or unavoidable."

The observation that *C. raymondhansorum* inhabits bromeliads was reinforced by researchers from the University of Glasgow (Ward 1996), who collected several specimens from *G. erectiflora* while searching for the golden tree frog, *Phyllodytes auratus*. Rudd (1996), also from the University of Glasgow, conducted a study of the "bromeliad-dwelling scorpion" which resulted in the collection of further specimens from bromeliads.

However, it appears that the view of this scorpion as a bromeliad specialist is nothing more than an artefact of diurnal collecting methods, which target bromeliads as a convenient place to search. The fact that most of the known specimens were located incidentally while searching for golden tree frogs supports this assertion. As has been found in other parts of the world (e.g., southern Africa), the habits and habitats of scorpions are best assessed nocturnally with the aid of UV light (Lamoral 1979). None of the four specimens of *C. raymondhansorum* collected by the author was found near a bromeliad: one retreated into a hole in a rotten tree stump, another into

a hole in a tree trunk, while the remaining specimens were found motionless on tree branches. Were these scorpions true bromeliad specialists, one would expect to have found them sitting on bromeliads. The behavior of *C. raymondhansorum* appears, in fact, to be fairly typical of a generalist arboreal scorpion, bromeliad leaf bases being one of many potential shelters into which such scorpions may opportunistically retreat.

Chactas raymondhansorum was found in sympatry with *T. tenuicauda* and *B. nitidus* on Mt. El Tucuche. None of the specimens was observed less than 1 m above ground level.

Material examined.—TRINIDAD AND TOBAGO: *Trinidad:* 2♂1♀, 1 subadult ♀, Mt. El Tucuche (summit), 8 July 1999, L. Prendini & I. Samad.

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LITERATURE CITED

Armas, L.F., de. 1974. Escorpiones del Archipiélago Cubano. 2. Hallazgo de género *Microtityus* (Scorpionida: Buthidae) con las descripciones de un nuevo subgénero y tres nuevas especies. Poeyana 132:1–26.

Armas, L.F., de. 1977. Nueva quetotaxia en escorpiones de la familia Buthidae (Arachnida, Scorpionida). Academia de Ciencias de Cuba, Miscelánea Zoológica 6:2–3.

Armas, L.F., de. 1988. Sinopsis de los escorpiones antillanos. Editorial Científico-Técnica, Habana. 102 pp.

Borelli, A. 1910. Descrizione di un nuovo scorpione del Venezuela. Bollettino dei Musei di Zoologia ed Anatomia Comparata della Reale Università di Torino 25:1–3.

Brignoli, P.M. 1985. On the correct dates of publication of the arachnid taxa described in some works by C.W. Hahn and C.L. Koch (Arachnida). Bulletin of the British Arachnological Society 6:414–416.

Bücherl, W. 1959. Escorpiões e escorpionismo no Brasil. X. Cátalogo da coleção escorpionica do Instituto Butantan. Memórias do Instituto de Butantan 29:255–275.

Bücherl, W. 1964. Distribução geografica dos aracnoides peconhentos temiveis (class Arachnomorpha, sub-class Arachnoidea, ordens Scorpiones e Araneida). Memórias do Instituto de Butantan 31:55–66.

Bücherl, W. 1967. Escorpiões, aranhas e escolopendromorfos da Amazônia. Pp. 5:111–125. *In* Atas do Simposio sôbre a Biota Amazônica. (H. Lent, ed.).

Bücherl, W. 1969. Giftige Arthropoden. Pp. 19(2):764–793. *In* Biogeography and Ecology in South America. Monographiae Biologicae. (E.J. Fittkau, ed.). W. Junk, Dordrecht.

Bücherl, W. 1971. Classification, biology and venom extraction of scorpions. Pp. 317–348. *In* Venomous Animals and their Venoms. Vol. III. (W. Bücherl & E. Buckley, eds.). Academic Press, New York.

Bücherl, W. 1978. Venoms of Tityinae. A. Systematics, distribution, biology, venomous apparatus, etc. of Tityinae; venom collection, toxicity, human accidents and treatment of stings. Pp. 48:371–379. *In* Arthropod Venoms. Handbook of Experimental Pharmacology. (S. Bettini, ed.). Springer-Verlag, New York.

Caporiacco, L. di. 1947. Diagnosi preliminari di specie nuove di Aracnidi della Guiana Brittanica raccolte dai professori Beccari e Romiti. Monitore Zoologico Italiano, Firenze 56:20–34.

Caporiacco, L. di. 1948. Arachnida of British Guiana collected in 1931 and 1936 by Professors Beccari and Romiti. Proceedings of the Zoological Society of London 118:607–747.

Caporiacco, L. di. 1951. Studi sugli Aracnidi del Venezuela raccolti della Sezione di Biología (Università Centrale del Venezuela). 1 Parte: Scorpiones, Opiliones, Solifuga y Chernetes. Acta Biológica Venezuelica 1:1–46.

Cekalovic, K.T. 1982 (1983). Estado actual de la colección arachnológica del Museo de Zoología de la Universidad de Concepción (M.Z.U.C.), parte Scorpiones. Memórias do Instituto de Butantan 46:187–192.

Couzijn, H.W.C. 1976. Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments. Netherlands Journal of Zoology 26:453–501.

Esquivel de Verde, M.A. 1969. Los Alacranes del Valle de Caracas (Scorpionida). Estudio de Caracas. Ed. de la Biblioteca de la Universidad Central de Venezuela 1:205–226.

Esquivel de Verde, M.A. & C.E. Machado-Allison. 1969. Escorpiones. Cuadernos Científicos: Dirección de Cultura. Universidad Central de Venezuela, Caracas. 53 pp.

Fet, V. & G. Lowe. 2000. Family Buthidae. Pp. 54–286. In Catalog of the Scorpions of the World (1758–1998). (V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder). New York Entomol. Soc., New York.

Flórez, E. 1991. Escorpiones de Colombia. Catálogo de Especies. Cespedesia 16–17:117–127.

Francke, O.F. & J. Boos. 1986. Chactidae (Scorpiones) from Trinidad and Tobago. Journal of Arachnology 14:15–28.

González-Sponga, M.A. 1971. Contribución al conocimiento sistemático y ecologico de Ananteris cussinii Borelli, 1910 (Scorpionida, Buthidae). Monografias Científicas "Augusto Pi Suñer" (Caracas, Instituto Pedagógico) 2:1–23.

González-Sponga, M.A. 1974a. Dos nuevas especies de alacranes del género Tityus en las cuevas venezolanas (Scorpionida, Buthidae). Boletín de la Sociedad Venezolana de Espeleología 5:55–72.

González-Sponga, M.A. 1974b. Broteochactas sanmartini (Scorpionida, Chactidae) nueva especie del río Caura, en la Guayana de Venezuela. Monografias Científicas "Augusto Pi Suñer" (Caracus, Instituto Pedagógico) 7:1–16.

González-Sponga, M.A. 1974c. Una nueva especie de escorpiones (Scorpionida, Chactidae) de la Amazonia de Venezuela. Acta Biológica Venezuelica 8:299–313.

González-Sponga, M.A. 1975. Broteochactas racenisi (Scorpionida, Chactidae) nueva especie de la Guyana Venezolana. Caribbean Journal of Science 6:123–135.

González-Sponga, M.A. 1978. Escorpiofauna de la región oriental del estado Bolívar, Venezuela. Trabajos científicos meritorios del Consejo Nacional de Investigaciones Científicas y Tecnológicas. Roto-impresos, Caracas. 216 pp.

González-Sponga, M.A. 1981. Seis nuevas especies del género Tityus en Venezuela (Scorpionida, Buthidae). Monografias Científicas "Augusto Pi Suñer" (Caracas, Instituto Pedagógico) 12:1–85.

González-Sponga, M.A. 1984. Escorpiones de Venezuela. Cuadernos Lagoven, Caracas. 128 pp.

González-Sponga, M.A. 1985. Tres nuevas especies de arácnidos de Venezuela (Scorpionida: Chactidae: Buthidae). Memoria de la Sociedad de Ciencias Naturales "La Salle" 45:25–45.

González-Sponga, M.A. 1989. Tres nuevas especies del género Tityus de Venezuela. Boletín de la Sociedad Venezolana de Ciencias Naturales 41:217–256.

González-Sponga, M.A. 1992. Arácnidos de Venezuela. Una nueva especie del género Broteochactas y redescripción de Broteochactas gollmeri (Karsch, 1879) (Scorpionida: Chactidae). Memoria de la Sociedad de Ciencias Naturales "La Salle" 52:53–64.

González-Sponga, M.A. 1996. Guía para identificar escorpiones de Venezuela. Cuadernos Lagoven, Caracas, 204 pp.

Hjelle, J.T. 1990. Anatomy and morphology. Pp. 9–63. In The Biology of Scorpions. (G.A. Polis, ed.). Stanford Univ. Press, Stanford, California.

Hummelinck, P.W. 1940. Scorpions. In Studies on the Fauna of Curaçao, Aruba, Bonaire, and the Venezuelan islands. (M. Nijhoff, ed.). 2:138–146. The Hague.

International Commission on Zoological Nomenclature. 1985. International Code of Zoological Nomenclature. 3rd ed. Univ. of California Press, Berkeley. 338 pp.

Kjellesvig-Waering, E.N. 1966. The scorpions of Trinidad and Tobago. Caribbean Journal of Science 6:123–135.

Kjellesvig-Waering, E.N. 1986. A restudy of the fossil Scorpionida of the world. Palaeontographica Americana 55:1–287.

Koch, C.L. 1844. Die Arachniden. 11:1–174. C.H. Zeh, Nürnberg.

Koch, C.L. 1850. Scorpionen. In Übersicht des Arachnidensystems. 5:86–92. C.H. Zeh, Nürnberg.

Kovařík, F. 1998. Stirí (Scorpions en tchèque). Madagaskar, Jihlava. 175 pp.

Kraepelin, K. 1894. Revision der Scorpione. II. Scorpionidae und Bothriuridae. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 11:1–248.

Kraepelin, K. 1895. Nachtrag zu Theil I der Revision der Scorpione. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 12:73–96.

Kraepelin, K. 1899. Scorpiones und Pedipalpi. Pp. 8:1–265. In Das Tierreich. (F. Dahl, ed.). R. Friedländer, Berlin.

Kraepelin, K. 1901. Catalogue des scorpions des

collections du Muséum d'histoire naturelle de Paris. Bulletin du Muséum National d'Histoire Naturelle, Paris 7:263–265.

Kraepelin, K. 1908. Die sekundären Geschlechtscharaktere der Skorpione, Pedipalpen und Solifugen. Mitteilungen aus dem Naturhistorischen Museum (2. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten) 25:181–225.

Kraepelin, K. 1912. Neue Beiträge zur Systematik der Gliederspinnen. II. Chactinae (Scorpiones). Mitteilungen aus dem Naturhistorischen Museum (2. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten) 29:43–88.

Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). Annals of the Natal Museum 23:498–783.

Lourenço, W.R. 1981 (1982). *Tityus gasci*, nouvelle espèce de scorpion Buthidae de Guyane française. Bulletin du Muséum National d'Histoire Naturelle, Paris 3:841–845.

Lourenço, W.R. 1982. Révision du genre *Ananteris* Thorell, 1891 (Scorpiones, Buthidae) et déscription de six espèces nouvelles. Bulletin du Muséum National d'Histoire Naturelle, Paris 4:119–151.

Lourenço, W.R. 1983. La faune des scorpions de Guyane Francaise. Bulletin du Muséum National d'Histoire Naturelle, Paris 5:771–808.

Lourenço, W.R. 1984a. Analyse taxonomique des scorpions du group *Tityus clathratus* Koch, 1845 (Scorpiones, Buthidae). Bulletin du Muséum National d'Histoire Naturelle, Paris 6:349–360.

Lourenço, W.R. 1984b. Notas taxonomicas sôbre *Tityus trinitatis* Pocock, 1897 (Scorpiones, Buthidae). Revista Brasileira da Biologia 44:15–19.

Lourenço, W.R. 1986a. Diversité de la faune scorpionique de la région amazonienne; centres d'endémisme; nouvelle appui à la théorie des refuges forestiers du Pléistocène. *In* Actas X Congress International Aracnologia, Jaca (España). (J.A. Barrientos, ed.). 1:231–237. Instituto Pirenaico de Ecología (C.S.I.C.) and Grupo de Aracnología (Assoc. Espanol Entomol.), Barcelona.

Lourenço, W.R. 1986b. Diversité de la faune scorpionique de la région amazonienne; centres d'endémisme; nouvelle appui à la théorie des réfuges forestiers du Pléistocène. Amazoniana 99:559–580.

Lourenço, W.R. 1991. La "Province" Biogéographique Guyanaise; étude de la biodiversité et des centres d'endémisme en vue de la conservation des patrimoines génétiques. Comptes Rendus Sommaires des Séances de la Société de Biogéographie 67:113–131.

Lourenço, W.R. 1992. Biogéographie des espèces du groupe naturel ≪*Tityus clathratus*≫ (Chelicerata, Scorpiones, Buthidae). Bulletin du Muséum National d'Histoire Naturelle, Paris (4)14:473–481.

Lourenço, W.R. 1993. A review of the geographical distribution of the genus *Ananteris* Thorell (Scorpiones: Buthidae), with description of a new species. Revista de Biología Tropical 41:697–701.

Lourenço, W.R. 1995. The remarkable discovery of a new and extinct species of *Tityus* from Martinique in Lesser Antilles (Chelicerata, Scorpiones, Buthidae). Anales del Instituto de Biología Universidad Nacional Autónoma de México, serie Zoologia 66:27–32.

Lourenço, W.R. 1997. Additions à la faune de scorpions néotropicaux (Arachnida). Revue Suisse de Zoologie 104:587–604.

Lourenço, W.R. & V.R.D. von Eickstedt. 1983. Présence du genre *Microtityus* (Scorpiones, Buthidae) au Brésil. Déscription de *Microtityus vanzolinii* new species. Revue Arachnologique 5:65–72.

Lourenço, W.R. & V.R.D. von Eickstedt. 1987. Contribução ao conhecimento taxonómico dos escorpiões associados ao grupo *Tityus melanostictus* Pocock, 1893 (Scorpiones, Buthidae). Memórias do Instituto de Butantan 49:87–95.

Lourenço, W.R. & D. Huber. 1999. Additions to the scorpion faunas of Trinidad and Tobago. Revue Suisse de Zoologie 106:249–267.

Mello-Leitão, C. de. 1931. Divisão e distribução do genero *Tityus* Koch. Annaes da Academia Brasileira de Ciências 3:119–150.

Mello-Leitão, C. de. 1932. Notas sôbre escorpiões Sul-Americanos. Arquivos do Museu Nacional, Rio de Janeiro 34:9–46.

Mello-Leitão, C. de. 1939. Revisão do genero *Tityus*. Physis (Buenos Aires) 17:57–76.

Mello-Leitão, C. de. 1945. Escorpiões Sul-Americanos. Arquivos do Museu Nacional, Rio de Janeiro 40:7–468.

Pocock, R.I. 1889. On *Isometrus americanus* (Linn.), with a description of a new species of the genus. Annals and Magazine of Natural History 4:53–59.

Pocock, R.I. 1893a. Notes on the classification of scorpions, followed by some observations on synonymy, with descriptions of new genera and species. Annals and Magazine of Natural History (6)12:303–330.

Pocock, R.I. 1893b. Contributions to our knowledge of the arthropod fauna of the West indies. Part I. Scorpiones and Pedipalpi, with a supplementary note upon the freshwater Decapoda of St. Vincent. Journal of the Linnean Society 24:374–409.

Pocock, R.I. 1897a. Report upon the Scorpiones and Pedipalpi obtained on the Lower Amazons by Messrs E.E. Austen and F. Pickard-Cambridge during the trip of Mr Siemens Steamship 'Faraday'. Annals and Magazine of Natural History (6)19:357–368.

Pocock, R.I. 1897b. Descriptions of some new spe-

cies of scorpions of the genus *Tityus*, with notes upon some forms allied to *T. americanus* (Linn.). Annals and Magazine of Natural History (6)19: 510–521.

Pocock, R.I. 1900. Myriopoda and Arachnida. In Report on a collection made by Messrs F.V. McConnell and J.J. Quelch at Mount Roraima in British Guiana. Transactions of the Linnean Society of London (Zoology) 2:64–71.

Roewer, C.F. 1943. Über eine neuerworbene Sammlung von Skorpionen des Natur-Museums Senckenberg. Senckenbergiana 26:205–244.

Rudd, S. 1996. Investigations into the habit of the bromeliad dwelling scorpion *Chactas raymondhansi*. Pp. 79–87. In Univ. of Glasgow Expedition to Trinidad, unpubl. research report. (R. Downie, M. Heath & C. Hambly, eds.). Univ. of Glasgow Exploration Soc., Glasgow.

Rudloff, J.P. 1994. Die Skorpionsfauna der Antillen (Arachnida: Scorpiones). Teil II. Arthropoda 2:16–34.

Santiago-Blay, J.A. 1985. *Microtityus dominicanensis*: a new scorpion from the Dominican Republic, West indies (Scorpiones, Buthidae). Entomological News 96:1–6.

Santiago-Blay, J.A., W. Schawaller & G.O. Poinar, Jr. 1990. A new specimen of *Microtityus ambarensis* (Scorpiones, Buthidae), fossil from Hispaniola: evidence of taxonomic status and possible biogeographic implications. Journal of Arachnology 18:115–117.

Scorza, J.V. 1954a. Contribución al estudio de los escorpiones venezolanos. Clave para la identificación de especies y consideraciones generales sobre los escorpiones domiciliarios. Archivos Venezolanos de Patología Tropical y Parasitología Médica 2:157–165.

Scorza, J.V. 1954b. Sistemática, distribución geográfica y observaciones ecológicas de algunos alacranes encontrados en Venezuela. Memoria de la Sociedad de Ciencias Naturales "La Salle" 14:179–214.

Scorza, J.V. 1954c. Expedición Franco-Venezolana del Alto Orinoco. Publicaciones zoológicas. Escorpiones del Alto Orinoco. Boletín de la Sociedad Venezolana de Ciencias Naturales 15:163–175.

Scorza, J.V. 1954d. Dos especies nuevas de alacranes de Venezuela. Novedades Científicas. Serie Zoologica: Contribuciones Ocasionales del Museo de Historia Natural "La Salle" 12:1–11.

Sissom, W.D. 1990. Systematics, biogeography and paleontology. Pp. 64–160. In The Biology of Scorpions. (G.A. Polis, ed.). Stanford Univ. Press, Stanford, California.

Sissom, W.D. 2000. Family Chactidae. Pp. 287–322. In Catalog of the Scorpions of the World (1758–1998). (V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder). New York Entomol. Soc., New York.

Sissom, W.D. & W.R. Lourenço. 1987. The genus *Centruroides* in South America (Scorpiones, Buthidae). Journal of Arachnology 15:11–28.

Sissom, W.D., G.A. Polis & D.D. Watt. 1990. Field and laboratory methods. Pp. 445–461. In The Biology of Scorpions. (G.A. Polis, ed.). Stanford Univ. Press, Stanford, California.

Smithe, F.B. 1974. Naturalist's Color Guide Supplement. The American Museum of Natural History, New York. 229 pp.

Smithe, F.B. 1975. Naturalist's Color Guide. The American Museum of Natural History, New York, unpaginated.

Smithe, F.B. 1981. Naturalist's Color Guide. Part III. The American Museum of Natural History, New York. 37 pp.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. Entomological News 81:297–316.

Vachon, M. 1973 (1974). Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. Bulletin du Muséum National d'Histoire Naturelle, Paris (3)140:857–958.

Vachon, M. 1977. Contribution à l'étude des scorpions Buthidae du nouveau monde. 1. Complément à la connaisance de *Microtityus rickyi* Kj.-W. 1956 de l'île de la Trinité. 2. Description d'un nouvelle espèce et d'un nouvelle genre mexicains: *Darchenia bernadettae*. 3. Clé de détermination des genres de Buthidae du nouveau monde. Acta Biológica Venezuelica 9:283–302.

Wagner, F.W. 1977. Descriptions of *Centruroides* Marx from the Yucatán Peninsula (Arachnida, Scorpionida, Buthidae). Bulletin of the Association for Mexican Cave Studies 6:39–47.

Ward, A. 1996. Some bromeliad-dwelling scorpions in Trinidad. Bulletin of the British Arachnological Society 77:10–11.

Waterman, J.A. 1950. Scorpions of the West Indies with special reference to *Tityus trinitatis*. Caribbean Medical Journal 12:167–177.

Weidner, H. 1959. Die entomologischen Sammlungen des Zoologischen Staatsinstitut und Zoologischen Museums Hamburg. I. Teil. Pararthropoda und Chelicerata. I. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 57:89–142.

Werner, F. 1939. Neu-Eingänge von Skorpionen im Zoologischen Museum in Hamburg. II. Teil. Festschrift zum 60. Geburtstage von Professor Dr. Embrik Strand, Riga 5:351–360.

Williams, S.C. 1980. Scorpions of Baja California, Mexico and adjacent islands. Occasional Papers of the California Academy of Sciences 135:1–127.

PHYLOGENETIC ANALYSIS OF PHALANGIDA (ARACHNIDA, OPILIONES) USING TWO NUCLEAR PROTEIN-ENCODING GENES SUPPORTS MONOPHYLY OF PALPATORES

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ABSTRACT. Recent phylogenetic studies of Opiliones have shown that Cyphophthalmi and Phalangida (= Palpatores + Laniatores) are sister groups, but higher relationships within Phalangida remain controversial. Current debate focuses on whether Palpatores (= Caddoidea + Phalangioidea + Ischyropsalidoidea + Troguloidea) is monophyletic or paraphyletic, with Ischyropsalidoidea + Troguloidea (= Dyspnoi) being more closely related to Laniatores. The latter hypothesis was favored in recent combined studies of ribosomal DNA and morphology. Here higher relationships within Phalangida are examined using two nuclear protein-encoding genes, elongation factor-1α (EF-1α) and RNA polymerase II (Pol II), from 27 opilion species representing seven superfamilies. Cyphophthalmi was used as the outgroup. Nucleotide and inferred amino acid sequences were analyzed using maximum-parsimony and maximum-likelihood methods. All analyses recovered Palpatores as the monophyletic sister group to Laniatores with moderate to strong empirical support. Most palpatorean superfamilies were also recovered, but relationships among them were ambiguous or weakly supported. A monophyletic Palpatores was also obtained when EF-1α and Pol II sequences were analyzed together with 18S and 28S rDNA sequences.

Keywords: Molecular systematics, elongation factor-1α, RNA polymerase II, Opiliones

Members of the arachnid order Opiliones (harvestmen, shepherd spiders, daddy long-legs, etc.) are abundant and often highly visible members of many terrestrial ecosystems. The group is estimated to encompass about 5000 species (Shear 1982). The basic biology of most opilions is unexplored; but the order is known to encompass substantial behavioral and morphological diversity, with much recent work focusing on the structure and evolution of mating systems (e.g., Macías-Ordóñez 1997; Martens 1993; Mora 1987, 1990, 1991; Ramires & Giaretta 1994) and the evolutionary morphology of genitalia (e.g., Martens 1976, 1980, 1986; Martens, Hoheisel & Götze 1981; Hoheisel 1980; Shultz 1998). An understanding of the phylogenetic relationships within Opiliones, and between Opiliones and other arachnid orders, is pivotal to further progress in these and other fields of arachnological research. However, many relationships are unclear and the focus of ongoing investigation and debate (e.g., Giribet et al. 1995, 1999; Giribet & Wheeler 1999; Shultz 1998, 2000).

The goal of the present study is to reconstruct phylogenetic relationships among major lineages within Opiliones using nucleotide and inferred amino-acid sequences from two nuclear protein-encoding genes, elongation factor-1α (EF-1α) and the largest subunit of RNA polymerase II (Pol II).

The monophyly of Opiliones is well established (Weygoldt & Paulus 1979; Shultz 1990), and three principal opilion groups are widely recognized, namely, Cyphophthalmi, Palpatores and Laniatores (Hansen & Sørensen 1904; Shear 1982). Cyphophthalmi (= Sironoidea) is a group of tiny (< 5 mm), hard-bodied and somewhat mite-like opilions characterized by many unique traits, such as a short male genital organ (spermatopositor), elevated ozopores (ozophores), a specialized spine on leg IV of males (adenostyle) and absence of a genital operculum (Shear 1982; Shultz 1998). Laniatores is a species-rich group of heavily sclerotized opilions that have radiated extensively in the neotropics and southeastern Asia (Shear 1982). Members of

this undisputedly monophyletic group are characterized by large, often raptorial palps, unsegmented ovipositors and other unique features. Palpatores is a morphologically diverse assemblage of four superfamilies (Caddoidea, Ischyropsalidoidea, Phalangioidea, Troguloidea) united by few morphological synapomorphies. Caddoidea and Phalangioidea include the typical "daddy longlegs" familiar to inhabitants of northern temperate regions and are characterized, in part, by well-developed coxal lobes (coxapophyses) and segmented ovipositors. Ischyropsalidoidea and Troguloidea are less familiar groups but encompass a substantial range of morphological diversity. They are characterized, in part, by reduced or absent coxapophyses, diaphanous cheliceral teeth and unsegmented ovipositors.

Opilion systematists have long debated the phylogenetic relationships of the three principal opilion lineages. Šilhavý (1961) placed Cyphophthalmi and Palpatores together as the sister group to Laniatores on the basis of the arrangement of tarsal claws; that is, claws of all legs are similar in Cyphophthalmi and Palpatores, but those of legs I and II differ from those of legs III and IV in Laniatores. A similar but more well-defended system was proposed by Martens and co-workers (Martens 1976, 1980, 1986; Hoheisel 1980; Martens et al. 1981). They also united Cyphophthalmi and Palpatores (= Cyphopalpatores) but argued that the palpatorean superfamily Troguloidea was the sister group to a clade comprising Cyphophthalmi and the remaining Palpatores, a system that rendered Palpatores a paraphyletic group. Their Cyphopalpatores hypothesis was based largely on original morphological studies of the ovipositor and penis, character systems that are uniquely derived in Opiliones. Consequently, the root and branching pattern of the tree proposed by Martens et al. was based on speculative character transformation series rather than inferences derived from outgroups. Shultz (1998) assessed the Cyphopalpatores concept through a parsimony-based morphological analysis of genitalic and non-genitalic characters using a generic taxon sample similar to that of Martens et al. and outgroups (i.e., scorpions and xiphosurans) to polarize non-genitalic characters. The results supported Cyphophthalmi as the sister group to Laniatores + Palpatores (= Phalan-

gida). Phalangida has also been supported by sperm ultrastructure (Juberthie & Manier 1978), arrangement of extrinsic pharyngeal muscles (Shultz 2000) and, especially, molecular sequence data. Giribet et al. (1999) using 18S and 28S ribosomal DNA and Shultz & Regier (unpublished) using EF-1α and Pol II amino acid sequences have recovered both Cyphophthalmi and Phalangida as monophyletic sister clades.

Recent morphological and molecular analyses appear to have established Phalangida as a monophyletic group, but there is debate concerning basal relationships within this group. These opilions are traditionally divided into the Palpatores and Laniatores, with Palpatores often divided into Dyspnoi (= Ischyropsalidoidea + Troguloidea) and Eupnoi (= Caddoidea + Phalangioidea) (Hansen & Sørensen 1904; Šilhavý 1961; Juberthie & Manier 1978; Shultz 1998). However, Giribet et al. (1999) conducted a phylogenetic analysis of Opiliones using 18S and 28S ribosomal DNA sequences and recovered two topologies, one favoring a monophyletic Palpatores and one favoring a paraphyletic Palpatores, with Dyspnoi being the sister group to Laniatores. The molecular characters alone did not strongly favor one hypothesis over the other, but a morphology-based analysis and the combined molecular-morphological study tended to support the Dyspnoi + Laniatores hypothesis. In a subsequent study, Giribet & Wheeler (1999) explored the significance of indels on the phylogenetic analysis of Opiliones. Using 18S ribosomal DNA sequences and morphological characters from Giribet et al. (1999), Giribet & Wheeler recovered Dyspnoi + Laniatores. However, given their exclusion of the 28S rDNA and use of a problematic morphology matrix (see Methods for details), it is probably best to regard Giribet & Wheeler's contribution as a demonstration of a new analytical method rather than a study of opilion relationships.

The present study examines higher relationships within Phalangida using nucleotide and amino-acid sequences from EF-1α and Pol II with the specific aim of testing the Dyspnoi + Laniatores hypothesis. Sequences were obtained from 27 opilion taxa representing the major opilion superfamilies (i.e., Sironoidea, Travunioidea, Gonyleptoidea, Phalangioidea, Caddoidea, Ischyropsalidoidea and Troguloi-

dea). Maximum-parsimony and maximum-likelihood analyses strongly and consistently recovered Palpatores and Laniatores as monophyletic sister groups under all character partitions, weighting schemes and analytical methods. This strong support for the monophyly of Palpatores contrasts with the ambiguous or weakly supported conclusions derived from studies of 18S and 28S ribosomal DNA and morphology (Giribet et al. 1999; Giribet & Wheeler 1999) or morphology alone (Shultz 1998). The represented superfamilies except Travunioidea also tended to be recovered, although support for Ischyropsalidoidea was weak, and it was not possible to conclude whether Dyspnoi and Eupnoi are monophyletic sister groups. Combined analysis of EF-1α and Pol II sequences with the 18S and 28S rDNA sequences of Giribet et al. (1999) also consistently recovered a monophyletic Palpatores. We regard these results as compelling evidence in support of the Palpatores hypothesis and against the Dyspnoi + Laniatores hypothesis. We suggest that future work on higher-level relationships within Opiliones focus an assessing the monophyly and relationships of superfamilies within Palpatores and Laniatores.

METHODS

Abbreviations.—Abbreviations used in the present study are as follows: bp, base pairs; nt1, first codon position; nt1noLR, nt1 data subset in which any characters that encode a leucine or arginine residue for any taxon are excluded at the homologous position in all taxa; nt1LR, nt1 data subset which includes any characters that encode a leucine or arginine residue for any taxon plus all other homologous characters in other taxa; nt2, second codon position; nt3, third codon position.

Terminal taxa and sequences.—Sequences of elongation factor-1α (EF-1α: 1092 bp) and the largest subunit of RNA polymerase II (Pol II: 1038 bp) were generated from 27 opilion species representing seven superfamilies. Specimens were collected alive, killed by immersion in 100% ethanol, and stored in 100% ethanol at −20 °C or −80 °C. Voucher specimens will be deposited in the U.S. National Museum of Natural History (Smithsonian Institution, Washington, DC). The list of specimens follows with GenBank accession numbers for EF-1α and Pol II, respectively, in

parentheses: Sironoidea: *Parasiro coiffaiti* Juberthie 1956 (Sironidae) (AF240852; AF241025 - AF241027), *Siro acaroides* (Ewing 1923) (Sironidae) (AF240855; AF241034 - AF241036). Travunioidea: *Equitius doriae* Simon 1880 (Triaenonychidae) (AF240867; AF241068 - AF241070), *Sclerobunus robustus* (Packard 1877) (Triaenonychidae) (AF240858; AF241042 - AF241044). Gonyleptoidea: *Gonyleptes fragilis* Mello-Leitão 1922 (Gonyleptidae: Gonyleptinae) (AF240868; AF241071 - AF241073), *Progonyleptoidellus striatus* (Roewer 1913) (Gonyleptidae: Progonyleptoidellinae) (AF240873; AF241086 - AF241088), *Sodreana sodreana* (Mello-Leitão 1922) (Gonyleptidae, Sodreaninae) (AF240879; AF241104 - AF241106), *Promitobates ornatus* (Mello-Leitão 1922) (Gonyleptidae, Mitobatinae) (AF240876; AF241095 - AF241097), *Discocyrtus areolatus* Piza 1938 (Gonyleptidae, Pachylinae) (AF240842; AF240994 - AF240996), *Laneosoares inermis* (B. Soares 1944) (Tricommatidae) (AF240871; AF241080 - AF241082), *Pseudobiantes japonicus* Hirst 1911 (Phalangodidae) (AF240874; AF241089 - AF241091), *Proscotolemon sauteri* Roewer 1916 (Phalangodidae) (AF240872; AF241083 - AF241085), *Scotolemon lespesi* (Lucas 1860) (Phalangodidae) (AF240878; AF241101 - AF241103). Caddoidea: *Caddo agilis* Banks 1892 (Caddidae) (AF240838; AF240980 - AF240982), *Caddo pepperella* Shear 1975 (Caddidae) (AF240863; AF241056 - AF241058). Phalangioidea: *Astrobunus grallator* Simon 1879 (Sclerosomatidae) (AF240862; AF241053 - AF241055), *Odiellus pictus* (Wood 1868) (Phalangiidae) (AF240850; AF241019 - AF241021), *Phalangium opilio* Linneaus 1758 (Phalangiidae) (AF240875; AF241092 - AF241094). Ischyropsalidoidea: *Ceratolasma tricantha* Goodnight & Goodnight 1942 (Ceratolasmatidae) (AF240864; AF241059 - AF241061), *Hesperonemastoma modestum* (Banks, 1894) (Ceratolasmatidae) (AF240869; AF241074 - AF241076), *Ischyropsalis luteipes* Simon 1872 (Ischyropsalididae) (AF240870; AF241077 - AF241079), *Sabacon imamurai* Suzuki 1964 (Sabaconidae) (AF240877; AF241098 - AF241100), *Taracus pallipes* Banks 1894 (Sabaconidae) (AF240881; AF241110 - AF241112). Troguloidea: *Di-*

cranolasma scabrum (Herbst 1799) (Dicranolasmatidae) (AF240866; AF241065 - AF241067), *Trogulus nepaeformis* (Scopoli 1763) (Trogulidae) (AF240880; AF241107 - AF241109), *Nipponopsalis abei* (Sato & Suzuki 1939) (Nipponopsalididae) (AF137391; AF138993 - AF138995), *Dendrolasma dentipalpe* Shear & Gruber 1983 (Nemastomatidae) (AF240865; AF241062 - AF241064).

Outgroups and phylogenetic framework.—The present study focuses on higher-level relationships within Phalangida and thus uses Cyphophthalmi as the outgroup. As summarized in the introduction, Opiliones is an unambiguously monophyletic group and recent phylogenetic analyses strongly support Cyphophthalmi and Phalangida as monophyletic sister groups. Results from molecular studies have been particularly convincing. Giribet et al. (1999) conducted an analysis of higher relationships within Opiliones and outgroups (i.e., Ricinulei, Solifugae, Scorpiones, Xiphosura) using 18S and partial 28S ribosomal DNA sequences and consistently recovered Cyphophthalmi and Phalangida as sister groups. Shultz & Regier (unpublished) used EF-1α and Pol II in a broad study of ordinal relationships within Arachnida and reconstructed Cyphophthalmi and Phalangida as monophyletic clades with high bootstrap support. Opiliones was rooted in the analysis with 26 outgroup species representing Xiphosura and all arachnid orders except Palpigradi. Taken together, these results effectively falsify the Cyphopalpatores hypothesis and strongly support the monophyly of Phalangida. It would have been possible in the present study to include all or some non-opilion arachnids, but these were excluded because inclusion of certain rapidly evolving arachnid lineages (especially Acari and Pseudoscorpiones) destabilizes even well-established relationships within Opiliones. We have therefore used the two species from Sironoidea (Cyphophthalmi) to root Phalangida.

Sequence data.—Procedures to generate sequence data sets have been published (Regier & Shultz 1997). In brief, total nucleic acids were isolated; cDNA copies of EF-1α and Pol II mRNA were reverse transcribed; dsDNA copies were amplified by PCR and subsequently gel isolated; the resulting PCR fragments were used as templates for another round of PCR amplification with nested primers; the resulting fragments were gel isolated and sequenced. If the resulting fragment concentration was too low to sequence directly, it was either concentrated or reamplified with M13 sequences present at the 5′ ends of all primer sequences. The same M13 sequences were also used as primers for thermal cycle/dideoxy sequencing. Sequencing reactions were fractionated and preliminary analyses were performed with Perkin-Elmer/ABI automated DNA sequencers. Automated DNA sequencer chromatograms were edited and contigs were assembled using the pregap and gap4 programs within the Staden software package (Staden et al. 1999). Sequences from different species were aligned and Nexus-formatted nucleotide data sets were constructed using the Genetic Data Environment software package (version 2.2, Smith et al. 1994). All sequences lacked indels. Amino acid data sets were inferred from nucleotide sequences using the universal nuclear genetic code option in MacClade, version 3.08 (Maddison & Maddison 1992).

Data analysis.—Maximum parsimony (MP) analyses of nucleotide and amino acid data sets were performed in PAUP*4.0 (Swofford 1998) using unordered, equally weighted characters. The following data sets were analyzed: all-nucleotide, nt1 + nt2, nt1noLR + nt2, nt3, amino acids. Amino acids were also analyzed using a "Protpars" step matrix constructed in MacClade. The step matrix consisted of transformation scores of "1" or "2" determined by the minimum number of nonsynonymous nucleotide changes separating particular codons. Serine codons that differed at nt1 were coded separately (termed "nondisjunct" in MacClade). Analysis consisted of a heuristic search using TBR branch swapping with random taxon addition (100 replications). Bootstrap values (Felsenstein 1985) were also obtained using heuristic searches (1000 replications each with 10 random-sequence addition replicates). The incongruence length difference test (Farris et al. 1995), implemented in PAUP* 4.0 as the partition homogeneity test (1000 replications), was used to test for the significance of conflict between genes and character partitions.

Maximum likelihood (ML) analyses of nucleotide data sets were performed with PAUP* 4.0 under the optimal GTR model of sequence evolution, the optimal model based on a series

of likelihood-ratio tests conducted according to Swofford et al. (1996: 430–438; see also Shultz & Regier 2000). Among-site rate variation was accommodated within the GTR model by likelihood estimations of separate rates for individual codon positions by gene and by fitting total likelihood-estimated character change to a gamma distribution with invariable sites estimated separately (Hasegawa, Kishino & Yano 1985). We call the former model GTR-ssr and the latter GTR + Γ + I. The GTR-ssr model was applied to total nucleotide data and the GTR + Γ + I model to the nt1 + nt2 and the nt1noLR + nt2 data sets.

As a first step in our exploration of tree space using ML analysis, we used an MP tree derived from analysis of amino acids as the input topology on which likelihood parameters were optimized. NNI branch swapping was then performed, and new likelihood parameters were estimated from the most likely topology. TBR branch swapping was conducted on the new tree and likelihood parameters were re-estimated. These parameters were then used as input for a heuristic search with NNI branch swapping and 100 random taxon additions. The parameters from the overall best tree were re-optimized. Bootstrap analyses were too computationally demanding to be performed in the same manner. Instead, the Neighbor Joining algorithm coupled with an ML-estimated distance matrix were used (1000 replications). For each bootstrapped data set, a ML distance matrix was calculated that assumed a minimum evolution objective function and that used identical parameters (i.e., rate matrix, base frequencies, α value, proportion of invariant sites) to those estimated from the ML topology of the original data set. Bootstrap values for the nt1 + nt2 and the nt1noLR + nt2 data sets were calculated in this manner.

ML analysis of the amino-acid data set was performed using the protml program within the MOLPHY software package (version 2.2, Adachi & Hasegawa 1994) and the empirical transition matrix compiled by Jones, Taylor & Thorton (1992). All 37681 amino acid parsimony trees within 4 steps of the minimum-length tree (= 354 steps) were read in batch into protml, and the tree with the highest likelihood score was selected. The significance of differences in the fit of individual data sets to

alternative topologies under both MP and ML criteria was assessed by the test of Kishino & Hasegawa (1989), using the "Tree Scores" option as implemented in PAUP* 4.0. Only fully dichotomous trees were compared; that is, single nodes (e.g., Dyspnoi + Laniatores) were constrained and the remaining set of unconstrained relationships was reoptimized. Percentage differences of all pairwise combinations of EF-1α and of Pol II amino acid and nt3 data sets were calculated in PAUP* 4.0. Average differences across the basal node of various groups were calculated by averaging all values across the basal dichotomy within a particular clade. Base compositions were calculated by gene and by codon position type using PAUP* 4.0.

Combined analyses with ribosomal DNA.—Unweighted MP analyses were conducted on data matrices that combined the 18S and 28S ribosomal sequences generated by Giribet et al. (1999) (15 opilions and 5 outgroups) with the EF-1α and Pol II sequences (27 opilions) generated in the present study. Two combined matrices were constructed. In the first, ribosomal data were combined with complete nucleotide sequences from EF-1α and Pol II for a total of 4329 characters (1117 parsimony-informative characters), and, in the second, the ribosomal data were combined with amino acids from EF-1α and Pol II for a total of 2909 characters (346 parsimony-informative characters). In both cases, the ribosomal sequences were aligned and edited as described in Giribet et al. (1999). Both matrices included 35 terminal taxa, which encompassed 15 taxa with both ribosomal and EF-1α + Pol II sequences, nine taxa with only ribosomal sequences, and 11 taxa with only EF-1α + Pol II sequences. Regions of the matrix lacking sequence data were treated as missing characters.

The specific strategy for combining ribosomal and protein-encoding sequences is presented below. The following five species were represented by both rDNA and protein-encoding sequences: *Parasiro coiffaiti* (GenBank accession nos.: 18S: U36999; 28S: U91495), *Equitius doriae* (18S: U37003, 28S: U91503), *Scotolemon lespesi* (18S: U37005, 28S: U91506), *Caddo agilis* (18S: U91487, 28S: U91502) and *Ischyropsalis luteipes* (18S: U37000, 28S: U91497). We also combined sequences from five pairs of closely related taxa,

specifically, *Siro rubens* Latreille 1804 (18S: U36998, 28S: U91494) was combined with EF-1α and Pol II sequences for *Siro acaroides*, *Odiellus troguloides* (Lucas 1847) (18S: X81441, 28S: U91500) was combined with *Odiellus pictus*, *Dicranolasma soerenseni* Thorell 1876 (18S: U37001, 28S: U91498) was combined with *Dicranolasma scabrum*, the nemastomatid *Centetostoma dubium* (Mello-Leitão 1936) (18S: U37002, 28S: U91499) was combined with *Dendrolasma dentipalpe*, and the pachyline gonyleptid *Pachyloides thorelli* Holmberg 1878 (18S: U37007, 28S: U91508) was combined with *Discocyrtus areolatus*. Taxa represented only by rDNA sequences included an unidentified *Stylocellus* Westwood 1874 (18S: U91485, 28S: U91496), an unidentified *Oncopus* Thorell 1876 (18S: U91488, 28S: U91504), *Maiorerus randoi* Rambla 1991 (18S: U37004, 28S: U91505), *Gnidia holnbergi* Soerensen 1912 (U37006, 28S: U91507), the solifuge *Eusimonia wunderlichi* Pieper 1977 (18S: U29492, 28S: none), the ricinuleid *Pseudocellus pearsei* (Chamberlin & Ivie 1938) (18S: U91489, 28S: none), the scorpion *Androctonus australis* C.L. Koch 1839 (18S: X77908, 28S: none), and the xiphosurans *Limulus polyphemus* (Linneaus 1758) (18S: U91490, 28S: U91492) and *Carcinoscorpius rotundicauda* (Latrieille 1802) (18S: U91491, 28S: U91493).

Giribet et al. (1999) had also presented a matrix of 45 morphological characters from an unreferenced literature review, but we did not include it in the combined analysis due to numerous ambiguities and inaccuracies. For example, palpal claws were coded as well developed in Sironoidea, but these claws are reduced compared to pedal claws (Hansen & Sørensen 1904; Shultz 1998). Two characters focusing on "fusion of abdominal tergites" were questionable, because males and females were coded separately, thereby making the characters non-independent. Metapeltidial cones were coded as "absent" in *Caddo* but are present (Shultz 1998). Internal longitudinal muscles of the ovipositor were coded as "present" in *Parasiro* and *Siro*; "reduced" in *Odiellus*, *Caddo*, *Dicranolasma*, *Pachyloides*, *Scotolemon* and *Centetostoma* but they are "absent" in sironoids, phalangioids, *Caddo* and *Dicranolasma* and well developed in *Centetostoma*, *Scotolemon* and other gonyleptoids

(Martens et al. 1981). Circular muscles of the ovipositor were coded as absent in *Odiellus* and *Caddo*, but they are present in phalangioids and *Caddo* (Martens et al. 1981). Given concerns about accuracy, the absence of source citations and the need to expand the matrix to include taxa not considered by Giribet et al. (1999), we chose not to include the morphological matrix in the combined study.

RESULTS

Pairwise differences and base composition.—Inferences of phylogenetic relationships among arthropods at taxonomic levels deeper than those in the present study have demonstrated that EF-1α and Pol II sequences retain phylogenetic signal, although the synonymous changes of nt3 can be very homoplasious due to overlapping substitutions. Across Opiliones, observed pairwise differences at nt2, at which all changes are non-synonymous, did not exceed 8.1% for either gene. By contrast, maximum observed pairwise differences at nt3 were 50.6% for EF-1α and 70.5% for Pol II, and were never less than 10% for either gene. These observations are consistent with the greater homoplasy at nt3 relative to nt2 (and nt1, in which changes are a mixture of synonymous and non-synonymous changes). For example, fitting nt1, nt2, and nt3 data sets to the topology shown in Fig. 1 resulted in overall Retention Indices of 0.6347, 0.8351, and 0.3825, respectively.

Chi-square tests of homogeneity across taxa revealed no significant heterogeneity ($P \gg 0.05$) in most partitions examined (i.e., nt1, nt2 and nt1noLR of both genes separately and combined), both with and without constant sites excluded. Exceptions were nt1 minus constant sites for Pol II, nt3 for Pol II, and those partitions that included nt3 of Pol II (i.e., all-nucleotides and nt3 combined), all of which showed highly significant base heterogeneity ($P < 0.0001$).

Phylogenetic analyses of EF-1α and Pol II.—Partition homogeneity tests of character partitions revealed no significant inconsistencies in the phylogenetic signals of EF-1α and Pol II, except in comparisons that included nt3 of Pol II (Table 1). Given these results, and uncertainties concerning the importance and utility of the partition homogeneity tests as an assay of combinability (Baker & DeSalle
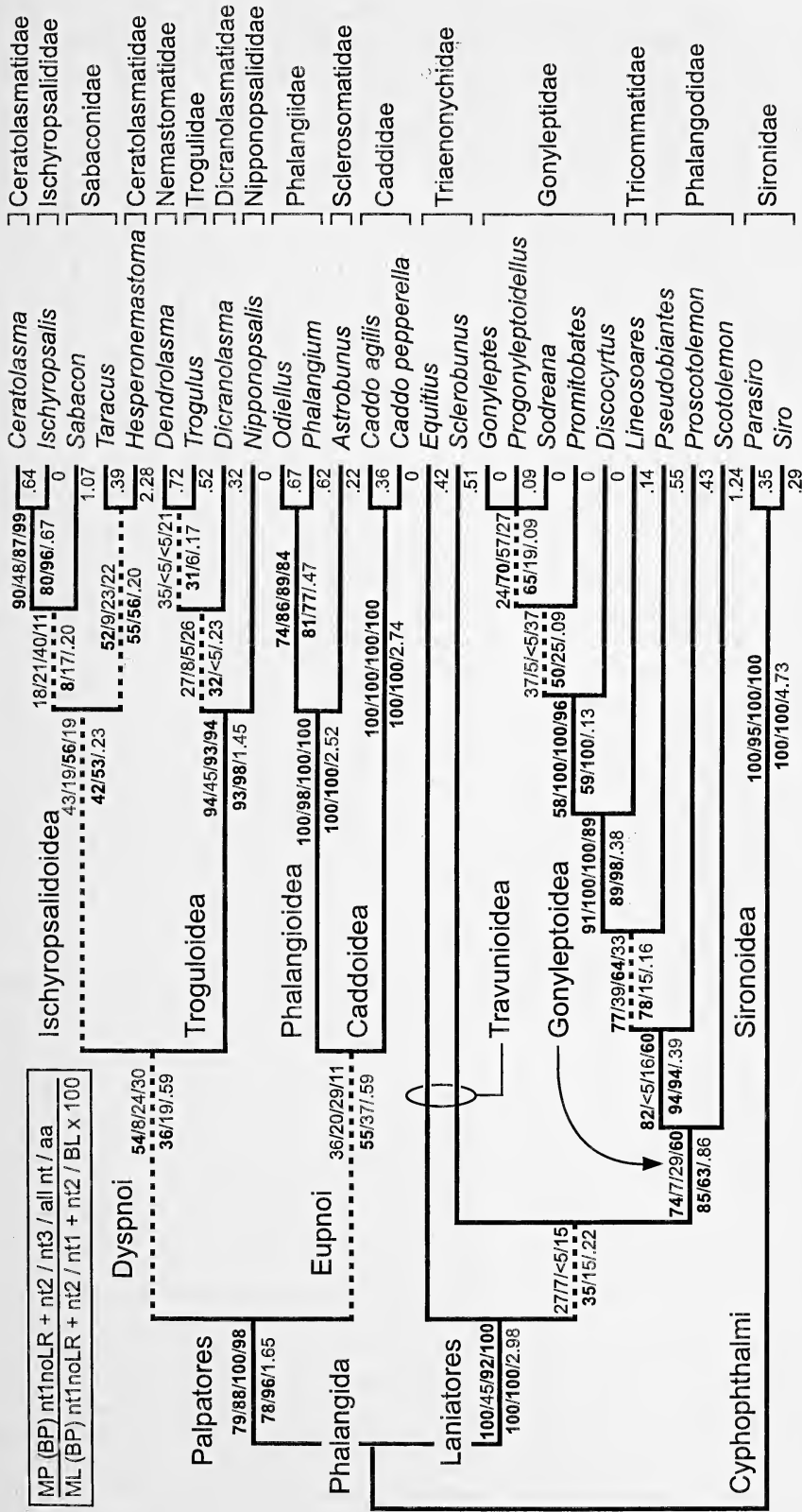
Figure 1.—Phylogenetic tree summarizing results from analyses of elongation factor-1α and RNA polymerase II for 27 opilion taxa. The depicted topology is the optimal tree derived from maximum-likelihood analysis of nt1noLR + nt2 using the GTR + Γ + I model (see text for details). Branches depicted by solid lines are considered well supported as indicated by empirical support (i.e., bootstrap value), stability and robustness to analytical method. Branches depicted by dashed lines are considered weakly supported by the same criteria. Numbers above internal branches are bootstrap percentages (BP) derived from maximum-parsimony (MP) analyses of nt1noLR + nt 2, nt3, all nucleotides and amino acids, respectively. The first two numbers below internal branches are bootstrap percentages derived from maximum-likelihood (ML) analyses of nt1noLR + nt2 and nt1 + nt2, respectively. The third number below internal branches and the only number under terminal branches are branch lengths (BL) derived from maximum-likelihood analysis of nt1noLR + nt2 multiplied by 100. Numbers in bold type indicate relationships recovered in the strict consensus of maximum parsimony trees or in the tree of highest likelihood.

1995; Cannatella et al. 1998), we performed combined analyses of all partitions.

Maximum-parsimony (MP) analyses of all character partitions (all-nucleotides, nt1 + 2, nt1noLR + nt2, nt3, amino acids, amino-acids-protpars) recovered the following higher clades within their respective minimal-length trees (bootstrap percentages [BP] in parentheses): Phalangida (100, 100, 100, 95, 100, 100); Laniatores (92, 99, 100, 45, 100, 100); Palpatores (100, 96, 79, 88, 87, 76); Troguloidea (93, 97, 94, 45, 94, 97); Caddoidea (100, 100, 100, 100, 100, 100) and Phalangioidea (100, 100, 100, 98, 100, 100). Ischyropsalidoidea was recovered by all-nucleotides (BP 56), nt1 + nt2 (BP 73), nt1noLR + nt2 (BP 43) and amino-acids-protpars (BP 30) but was recovered as a paraphyletic group by nt3 and amino acids. Dyspnoi (= Troguloidea + Ischyropsalidoidea) was recovered by all-nucleotides (BP 24), nt1 + nt2, (BP 59), nt1noLR + nt2 (BP 54), and amino-acid-protpars (BP 47). Eupnoi (= Caddoidea + Phalangioidea) was recovered by nt1noLR +nt2 (BP 36) within a subset of 20 MP trees. Gonyleptoidea was recovered by all-nucleotides, nt1noLR + nt2, amino acids, and amino-acids-protpars with weak-to-moderate bootstrap support (i.e., 29–74%). Travunioidea was recovered as a paraphyletic group with *Equitius* being the sister group to Gonyleptoidea and/or occurring within Gonyleptoidea.

The all-nucleotide and nt1 + nt2 data sets significantly preferred a monophyletic Palpatores over the MP clade constrained to a monophyletic Laniatores + Dyspnoi (*P* values ranged from 0.015 to 0.028), according to the test of Kishino & Hasegawa (1989); the other data sets were indecisive.

The ML topology recovered by analysis of the nt1noLR + nt2 data set is shown in Fig. 1. All maximum likelihood analyses (three models of nucleotide substitution and four data subsets, see Methods) recovered the following clades in their ML topologies (BP values for analysis of nt1 + nt2 and nt1nlLR + nt2, respectively, are in parentheses): Phalangida (100, 100), Laniatores (100, 100), Palpatores (96, 78), Troguloidea (98, 93), Gonyleptoidea (63, 85), Phalangioidea (100, 100), Caddoidea (100, 100), and Ischyropsalidoidea (53, 42). Eupnoi (37, 55) was recovered by all three nucleotide data sets. Dyspnoi (19, 36) was recovered only by the nt1noLR + nt2

data set. ML analysis of amino acids recovered Phalangida, Laniatores, Palpatores, Troguloidea, Caddoidea, Phalangioidea, and Gonyleptoidea.

Combined analyses.—Combined unweighted MP analyses of 18S + 28S rDNA and EF-1α + Pol II sequences strongly and consistently corroborated the monophyly of Palpatores (Fig. 2), the result favored by analysis of EF-1α + Pol II alone, not the Dyspnoi + Laniatores hypothesis that tended to be recovered by the rDNA data analyzed alone (Giribet et al. 1999). The strict consensus of 360 trees (length, 6067; CI, 0.31; RI, 0.48) derived from analysis of ribosomal and protein-encoding DNA included Opiliones, Phalangida, Laniatores, Palpatores, Dyspnoi and all represented opilion superfamilies (except Travunioidea) but did not recover Eupnoi (Fig. 2A). The Dyspnoi + Laniatores hypothesis was recovered in only 5% of bootstrap replicates and required 30 additional steps for recovery by parsimony analysis. Strict consensus of 78 trees (length, 865; CI, 0.54; RI, 0.75), derived from MP analysis of ribosomal DNA and EF-1α + Pol II amino acids included the same major opilion clades listed above but also recovered Eupnoi (Fig. 2B). The Dyspnoi + Laniatores hypothesis was recovered in only 5% of bootstrap replicates and required 10 additional steps for recovery by parsimony.

DISCUSSION

Status and future of higher relationships in Opiliones.—Recent phylogenetic analyses clearly indicate that Opiliones consists of two clades, Cyphophthalmi and Phalangida (Giribet et al. 1999; Shultz 1998; Shultz & Regier unpubl. data). Results from analysis of elongation factor-1α (EF-1α) and RNA polymerase II (Pol II), both alone and combined with 18S and 28S rDNA, strongly support the monophyly of Palpatores and Laniatores and are inconsistent with the recently proposed Dyspnoi + Laniatores hypothesis (Giribet et al. 1999, Giribet & Wheeler 1999). Molecular data examined thus far have consistently recovered three palpatorean superfamilies (Caddoidea, Phalangioidea, Troguloidea) as monophyletic groups (Giribet et al. 1999; present study), but monophyly of the remaining superfamily, Ischyropsalidoidea, is more problematic. This superfamily was recovered by
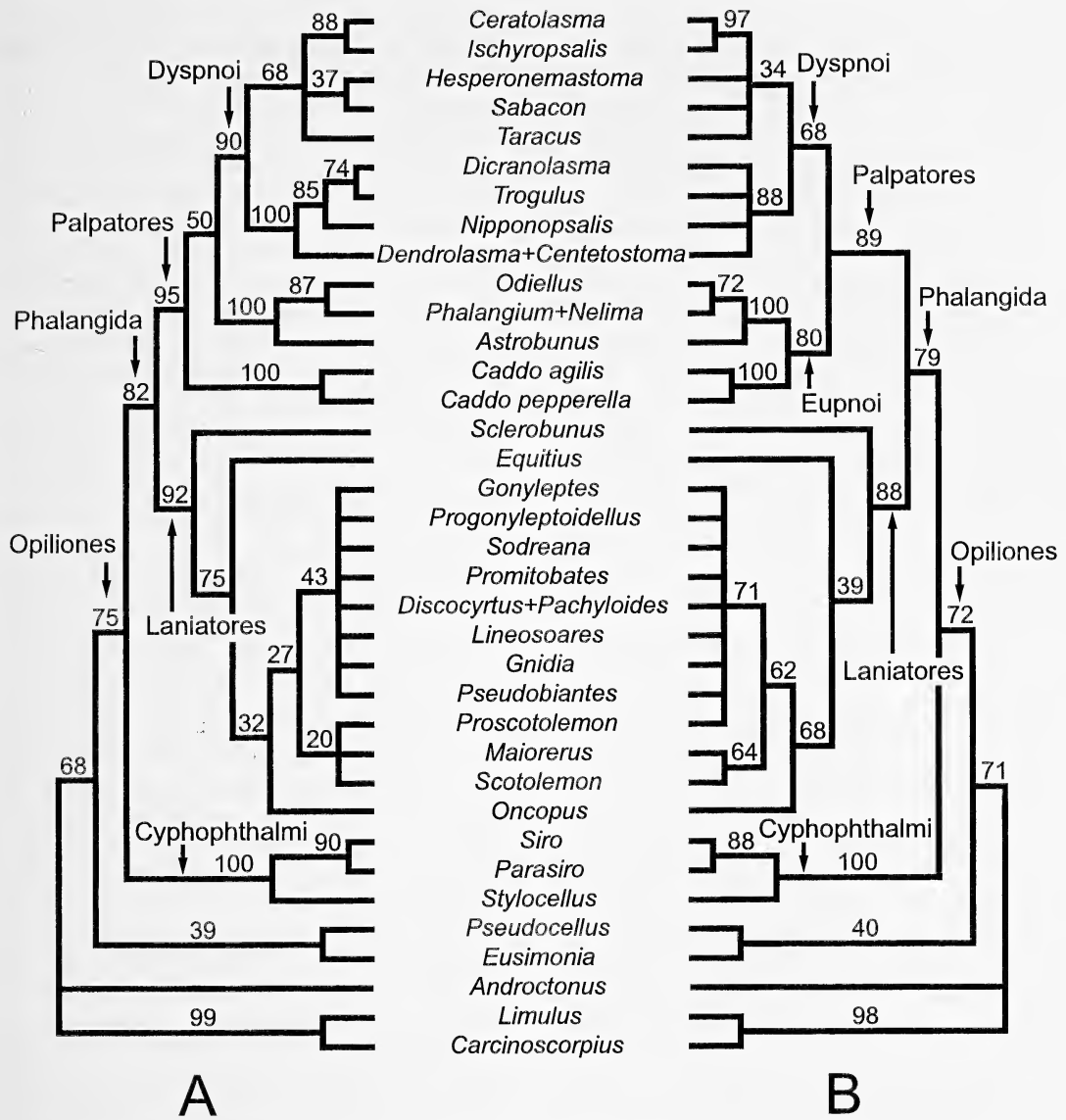
Figure 2.—Strict consensus trees derived from combined, unweighted maximum parsimony analyses of 18S rDNA, 28S rDNA, EF-1α and Pol II. A. Strict consensus of 360 trees derived from analysis of rDNA and EF-1α + Pol II nucleotides. B. Strict consensus of 78 trees derived from analysis of rDNA and EF-1α + Pol II amino acids. Numbers above internal branches are bootstrap percentages.

EF-1α and Pol II in only a few analyses with low bootstrap support (Fig. 1) and in both combined analyses with moderate support (Fig. 2). The traditional grouping of Caddoidea and Phalangioidea into Eupnoi and Ischyropsalioidea and Troguloidea into Dyspnoi could be neither falsified nor confirmed by EF-1α and Pol II, but they are both strongly supported in the combined analysis of 18S and 28S rDNA conducted by Giribet et al. (1999).

Based on the present study, it appears that phylogenetic signal within EF-1α and Pol II can resolve the deepest nodes within opilion phylogeny but become less useful at lower taxonomic levels. Specifically, relationships among and within superfamilies are largely unresolved by these two genes. This suggests that progress in opilion systematics will require the development of new genes, especially those that have evolved at a greater rate

than the two examined here as well as renewed efforts to search for informative morphological characters. Expanded taxon sampling is also important, and particular emphasis should be placed on sampling representatives from basally divergent lineages of each well-defined opilion clade. These include, but are not limited to, *Crosbycus* from Ischyropsalidoidea, neopilionids from Phalangioidea, acropsopilionids from Caddoidea and the travunioid families from Laniatores.

Relationships within Ischyropsalidoidea.—Ischyropsalidoidea is a morphologically diverse group encompassing three families (Ischyropsalididae, Sabaconidae, Ceratolasmatidae), but the monophyly of the superfamily is not well established. Shear (1986) united the ischyropsalidoids with four synapomorphies, namely, metapeltidial cones, unsegmented ovipositor, reduced palpal claw and presence of male cheliceral glands. However, metapeltidial cones are also present in Caddoidea (*Caddo*) and the remaining characters occur in some or all members of Troguloidea (Shultz 1998). Further, our molecule-based results do not support Shear's (1986) system of ischyropsalidoid families (Fig. 3A), but neither do they strongly conflict with it. Specifically, our analyses consistently recovered an *Ischyropsalis* + *Ceratolasma* grouping and frequently but weakly placed the ceratolasmatid *Hesperonemastoma* as the sister group to one or both sabaconids (Fig. 1). These results suggest that Ceratolasmatidae and Sabaconidae are not natural groups, although the evidence is weak. Still, para- or polyphyly of the two families is a hypothesis to be tested and is compatible with several other lines of evidence. First, few morphological characters support monophyly of the morphologically diverse Ceratolasmatidae (= *Acuclavella*, *Ceratolasma*, *Crosbycus*, *Hesperonemastoma*). Shear's (1986) diagnosis of the family includes no unique features and most characters have multiple states within the family (e.g., ". . . pairs of tubercles on scutum . . . high and acute, or blunt and appressed . . . or absent," "chelicerae with or without glands in males"; "palpi long, with . . . or short, without . . . plumose setae") (p. 13). Second, monophyly of Sabaconidae can also be questioned, although it is substantially more convincing than Ceratolasmatidae. Potential sabaconid synapomorphies include deep invagination in anterior

midline of carapace, reduced sclerotization, and enlarged palpal tibia and tarsus (Shear 1986). The first of these appears to be unique to the family, but the second seems to depend on a priori suppositions of character transformation. The third character is undoubtedly derived and clearly expressed in *Sabacon*, but is less obvious in *Taracus*, especially when the palps are compared to those of *Hesperonemastoma* (original observations). Thus, Sabaconidae is a probable but not unambiguously demonstrated family. Third, in his re-description of *Ceratolasma*, Gruber (1978) noted two phenetic groupings of taxa within Ischyropsalidoidea that are broadly congruent with our findings. Specifically, *Ceratolasma* and *Ischyropsalis* share a "prominent sternum, large labium, palpi without plumose setae, but with numerous microtrichia, and also a complex midgut anatomy" (p. 109). He also noted that *Hesperonemastoma* is similar to sabaconids in having "less developed sterna, small labia, palpi with extensive development of plumose setae and reduction of the microtrichial cover" and simpler midgut anatomy. Admittedly, both lists are mosaics of primitive and derived traits, and more intensive morphological and molecular analyses are needed to make progress in ischyropsalidoid systematics. The molecular data are open to criticism in that relationships among the relevant taxa are unstable and *Hesperonemastoma* appears to have undergone more rapid molecular evolution than other ischyropsalidoids, which may account for the ambiguity.

Relationships within Troguloidea.—In contrast to ischyropsalidoids, the troguloids are a well-defined, monophyletic group. Martens (Martens 1980, 1986; Martens et al. 1981; Martens & Suzuki 1966) and Shear & Gruber (1983) proposed several synapomorphies, including a penis with two longitudinal muscles, unique unsegmented ovipositor, fusion of sternum and leg coxae, clavate palpal setae, and reduced palpal claws. Only the latter is open to question, as reduced palpal claws are also present in ischyropsalidoids. The present study included one representative from each of the four troguloid families (Nipponopsalididae, Nemastomatidae, Dicranolasmatidae, Trogulidae) and our results strongly supported the monophyly of the superfamily under all character partitions and analytical methods (Fig. 1). However, relationships with-

in Troguloidea were ambiguous. Shear & Gruber (1983) regarded Dicranolasmatidae and Nemastomatidae as sister groups on the basis of one character (penis muscles with long tendons) but did not propose relationships between this clade, Trogulidae and Nipponopsalididae. Shultz (1998) proposed dicranolasmatids and trogulids as sister groups based on heavy sclerotization and anteriorly projecting eye tubercle or "hood" in these taxa. Our molecular data do not strongly support any phylogenetic arrangement among the troguloid families, although there was a tendency to recover the nemastomatid "Dendrolasma" as the sister group to the remaining representatives.

ACKNOWLEDGMENTS

LITERATURE CITED

Adachi, J. & M. Hasegawa. 1994. Programs for Molecular Phylogenetics. Version 3.3. Institute of Statistical Mathematics.

Baker, R.H. & R. DeSalle. 1997. Multiple sources of character information and the phylogeny of Hawaiian drosophilids. Systematic Biology 46:654–673.

Cannatella, D.C., D.M. Hillis, P.T. Chippindale, L. Weigt, A.S. Rand & M.J. Ryan. 1998. Phylogeny of frogs of the *Physalaemus pustulosus* species group, with an examination of data incongruence. Systematic Biology 47:311–335.

Farris, J.S., M. Källersjö, A.G. Kluge & C. Bult. 1995. Constructing a significance test for incongruence. Systematic Biology 44:570–572.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39:783–791.

Giribet, G., S. Carranza & C. Ribera. 1995. Molecular phylogeny of Opiliones based on 18S rDNA sequences. P. 219. *In* Proceedings of the 15th European Colloquium of Arachnology. (V. Růžička, ed.). Institute of Entomology, České Budějovice.

Giribet, G., M. Rambla, S. Carranza, M. Riutort, J. Baguñà & C. Ribera. 1999. Phylogeny of the arachnid order Opiliones (Arthropoda) inferred from a combined approach of complete 18S, partial 28S ribosomal DNA sequences and morphology. Molecular Phylogenetics and Evolution 11:296–307.

Giribet, G. & W.C. Wheeler. 1999. On gaps. Molecular Phylogenetics and Evolution 13:132–143.

Gruber, J. 1978. Redescription of *Ceratolasma tricantha* Goodnight and Goodnight, with notes on the family Ischyropsalidae (Opiliones, Palpatores). Journal of Arachnology 6:105–124.

Hansen, H.J. & W. Sørensen. 1904. On Two Orders of Arachnida. Cambridge Univ. Press, Cambridge.

Hasegawa, M., H. Kishino & T. Yano. 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22:160–174.

Hoheisel, U. 1980. Anatomie und taxonomische Bedeutung der Legeröhre der Opiliones. Verhandlungen der 8. Internationale Arachnologische Kongress, 1980, Wien 8:315–318.

Jones, D.T., W.R. Taylor & J.M. Thorton. 1992. The rapid generation of mutation data matrices from protein sequences. Computer Applications in the Biosciences 8:275–287.

Juberthie, C. & J.-F. Manier. 1978. Étude ultrastructural comparée de la spermiogenèse des opilions et son intérêt phylétique. Symposia of the Zoological Society of London, No. 42:407–416.

Kishino, H. & M. Hasegawa. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. Journal of Molecular Evolution 29:170–179.

Macías-Ordóñez, R. 1997. The Mating System Of *Leiobunum vittatum* Say 1821 (Arachnida: Opiliones: Palpatores): Resource Defense Polygyny In The Striped Harvestman. Ph.D. dissertation, Lehigh University.

Maddison, W.P. & D.R. Maddison. 1992. MacClade: Analysis of phylogeny and character evolution. Version 3. Sinauer Associates: Sunderland, Massachusetts.

Martens, J. 1976. Genitalmorphologie, System und Phylogenie der Weberknechte (Arachnida: Opiliones). Entomologica Germanica 3:51–68.

Martens, J. 1980. Versuch eines phylogenetischen Systems der Opiliones. Verhandelungen der 8. Internationale Arachnologische Kongress, 1980, Wien 355–360.

Martens, J. 1986. Die Grossgliederung der Opiliones und die Evolution der Ordnung (Arachnida). Actas X Congress International Arachnology, Jaca/España, I:289–310.

Martens, J. 1993. Further cases of paternal care in

Opiliones (Arachnida). Tropical Zoology 6:97–107.

Martens, J., U. Hoheisel & M. Götze. 1981. Vergleichende Anatomie der Legeröhren der Opilions als Beitrag zur Phylogenie der Ordnung (Arachnida). Zoologischer Jahrbücher Anatomie 105:13–76.

Martens, J. & S. Suzuki. 1966. Zur systematischen Stellung ostasiatischer Ischyropsalididen-Arten (Arachnoidea, Opiliones, Ischyropsalididae). Annotationes Zoologicae Japonenses 39:215–221.

Mora, G. 1987. Male Egg-guarding In The Neotropical Harvestman Zygopachylus albomarginis (Opiliones: Gonyleptidae). M.S. thesis, University of Florida, Gainesville.

Mora, G. 1990. Paternal Care In A Neotropical Harvestman, Zygopachylus albomarginis (Arachnida: Opiliones: Gonyleptidae). Animal Behaviour 39:582–593.

Mora, G. 1991. Site-based mating system in a tropical harvestman. Ph.D. dissertation, University of Florida, Gainesville.

Ramires, E.N. & A.A. Giaretta. 1994. Maternal care in a neotropical harvestman, Acutisoma proximum (Opiliones, Gonyleptidae). Journal of Arachnology 22:179–180.

Regier, J.C. & J.W. Shultz. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. Molecular Biology and Evolution 14:902–913.

Shear, W.A. 1982. Opiliones. Pp. 104–110. In Synopsis and Classification of Living Organisms, Vol. 2. (S.P. Parker, ed.). McGraw-Hill, New York.

Shear, W.A. 1986. A cladistic analysis of the opilionid superfamily Ischyropsalidoidea, with descriptions of the new family Ceratolasmatidae, the new genus Acuclavella, and four new species. American Museum Novitates, No. 2844:1–29.

Shear, W.A. & J. Gruber. 1983. The opilionid subfamily Ortholasmatinae (Opiliones, Troguloidea, Nemastomatidae). American Museum Novitates, No. 2757:1–65.

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6:1–38.

Shultz, J.W. 1998. Phylogeny of Opiliones (Arachnida): An assessment of the "Cyphopalpatores" concept. Journal of Arachnology 26:257–272.

Shultz, J.W. 2000. Skeletomuscular anatomy of the harvestman Leiobunum aldrichi (Weed 1893) (Arachnida: Opiliones: Palpatores) and its evolutionary significance. Zoological Journal of the Linnean Society 128:401–438.

Shultz, J.W. & J.C. Regier. 2000. Phylogenetic analysis of arthropods using two nuclear protein-encoding genes supports a crustacean + hexapod clade. Proceedings of the Royal Society of London B 267:1011–1019.

Šilhavý, V. 1961. Die Grundsätze der modernen Weberknechttaxonomie und Revision des bisherigen Systems der Opilioniden. Verhandlungen der 11. Internationaler Kongress für Entomologie, 1960, Wien 1:262–267.

Smith, S.W., R. Overbeek, C.R. Woese, W. Gilbert & P.M. Gillevet. 1994. The genetic data environment and expandable GUI for multiple sequence analysis. Computer Applications in the Biosciences 10:671–675.

Staden, R., K.F. Beal & J.K. Bonfield. 1999. The Staden package, 1998, In Bioinformatics Methods and Protocols. (S. Misener & S. Krawetz, eds.). The Humana Press, Inc., Totowa, New Jersey. 512 pp.

Swofford, D.L. 1998. PAUP* 4.0 beta version. Sinauer Associates, Sunderland, Massachusetts.

Swofford, D.L., G.J. Olsen, P.J. Waddell & D.M. Hillis. 1996. Phylogenetic inference. Pp. 407–514. In Molecular Systematics, 2nd ed. (C. Moritz & B.K. Mable, eds). Sinauer Associates, Sunderland, Massachusetts.

Weygoldt, P. & H.F. Paulus. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. Zeitschrift für zoologische Systematik und Evolutionsforschung 17:85–116, 77–200.

DESCRIPTION OF *HAKKA*, A NEW GENUS OF JUMPING SPIDER (ARANEAE, SALTICIDAE) FROM HAWAII AND EAST ASIA

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ABSTRACT. We describe a new genus for a jumping spider that was originally placed in the large genus *Menemerus* Simon 1868, from which the new genus is clearly different. They were later reclassified as *Icius*, then as *Pseudicius*, and still later as *Salticus*. These initial classifications were repeated by a number of authors. The distinctive features of the male, and somewhat ambiguous features of the female, do not fit any known genus; and this species is here assigned to the new genus *Hakka*.

Keywords: *Hakka*, *Salticus*, *Menemerus*, Hawaii, Salticidae

Like many other elements of the Hawaiian Islands, the jumping spiders of the islands are poorly known. Much of the known fauna consists of genera whose origin can be traced from either Asia or North America. This paper discusses a species found in Hawaii that was previously known under several different generic names—from a few specimens only—from China, Korea and Japan. One specimen was recorded in Hawaii in 1923, and we have recently collected two more. It is not known whether they are incidental recent arrivals (although the three specimens were collected over a period of 74 years) or have populations established there.

Hakka new genus

Discussion.—Assigning these salticid spiders to a genus has always created a problem. Although they have never been described as a separate genus, they were originally placed in the large genus *Menemerus* Simon 1868 (Doenitz & Strand in Bösenberg & Strand 1906), from which they are clearly different. Prószyński (1976) reclassified them first to *Icius* Simon 1876, subsequently correcting himself and re-interpreting them as *Pseudicius* (Prószyński 1987). Wesolowska (1981) interpreted the structure of the epigynum as resembling the genus *Salticus* Latreille 1804 and described the female as *Salticus koreanus* Wesolowska. These initial classifications were

later repeated by a number of authors. The fact is that the distinctive features of the male, and somewhat ambiguous features of the female, do not fit any known genus; and this species deserves delimitation to its own genus. There are no direct biological observations confirming the matching of males and females of this species; however, persistent interpretation of that matching by a number of authors deserves following until proven otherwise.

Diagnosis.—*Hakka* is a unidentate salticid with two prolateral cheliceral teeth, without patellar spines, and without lateral spines on metatarsi I and II. These same characters occur in the genera with which it has been confused—*Icius*, *Menemerus*, *Pseudicius*, and *Salticus*, but they do separate *Hakka* from many other salticid genera. The absence of stridulatory spines from the carapace and microspines from femur I, and presence of 5–6 ventral spines on tibia I clearly separate *Hakka* from *Pseudicius*. The latter has the stridulatory spines and, on tibia I, normally 0–3 spines that are usually much reduced in length and often thickened basally. *Pseudicius* differs also by having a long, flat, relatively narrow carapace, and large robust first legs with tibia I more-or-less swollen, and with unusually long trichobothria, usually bent at a distinct angle. From *Salticus*, *Hakka* is distinguished by the absence of elongate male chelicerae,

the presence of ventral spines on tibiae I and II, the elongate bulb of the male palp overlapping the tibia proximally, and the medium-long sinuous embolus (Figs. 3, 4). The epigynum is less sclerotized than in *Salticus*; and the epigynal ducts run forward from the copulatory openings, then turn back to the spermathecae (Figs. 6, 7). The typical *Salticus* color pattern of white lines of scale-like hairs is absent. *Icius* differs by having a proportionately longer, somewhat oblong carapace (shorter and more ovate in *Hakka*) and abdomen, the palpal bulb narrowing anteriorly, and a distinct color pattern, consisting in part of scale-like hairs. *Menemerus*, the genus in which *H. himeshimensis* was originally placed, has a flatter, broader cephalothorax and abdomen. Also, the male palp of *Menemerus* has the tibia and patella short and broad, often as broad as the cymbium, and a broad crescentic femur; the RTA is large, the embolar base wide and separated by a groove from the rest of the bulb: the embolus is accompanied by a membranous conductor-like portion. Epigynal openings lead directly into a bursa by a very short thick-walled duct to a second chamber. But in *Hakka* there is no membranous part in the male palp, and the bulb and epigynal ducts, as described above, differ strikingly.

Distribution.—Previously known from China, Japan, North Korea, and now, Hawaii.

Etymology.—Named for a group of Chinese people, members of which were brought to Hawaii as laborers on sugar cane plantations in the middle of 19th century (described in the book "Hawaii" by James Michener). For nomenclatorial purpose the name is considered to be female.

Type species.—*Menemerus himeshimensis* (Doenitz & Strand, in Bösenberg & Strand 1906).

Hakka himeshimensis (Doenitz & Strand)
(in Bösenberg & Strand 1906) new
combination
Figs. 1–7

Note: The type specimens, housed in Stuttgart, were destroyed during World War II.

Menemerus himeshimensis Doenitz & Strand, in Bösenberg & Strand 1906: 395–396, table 8, fig. 116; table 14, fig. 309.

Menemerus himeshimensis: Yaginuma 1970: 67; 1986a: 234, fig. 130.2.
Icius himeshimensis: Prószyński 1976: map 105.
Salticus koreanus Wesolowska 1981: 78, figs. 102–105 (Female holotype from North Korea: Nampho, prov. Phyongan-namdo, deposited at Muzeum i Instytut Zoologii, PAN, Warsaw, Poland, examined).
Icius himeshimensis: Bohdanowicz & Prószyński 1987:. 66, 67, figs. 65, 66.
*Pseudicius himeshimensis:* Prószyński 1987: 51 (transfer from *Menemerus, Icius*).
Icius himeshimensis: Chikuni 1989: 151, fig. 22.
Pseudicius himeshimensis: Peng, Xie & Xiao 1993: 191, 192, figs. 667, 670.

Description.—*Male:* Measurements ($n = 1$): total length 6.98, length of eye field 1.32, height of cephalothorax 1.42, width of eye field at eyes I 1.80, width of eye field at eyes III 1.80, width of cephalothorax at eyes III 2.28, maximum width of cephalothorax 2.64, length of flat surface of cephalothorax 0.96, length of abdomen 3.72. Body and legs uniformly dark brown, without any contrasting pattern. Cephalothorax relatively broad (broadest posteriorly) and low; eye field rectangular, indistinctly shorter than broad, posterior sloping part of cephalothorax short. Covered with sparse, inconspicuous adpressed lighter setae; longer setae, now reddish, stand up diagonally beneath lateral eyes. There is no row of tubercles with spines beneath the lateral eyes. Eyes I large, the diameter of median eyes almost twice the size of the lateral eyes. Eyes I surrounded by colorless, slightly reddish setae; setae above eyes longer; clypeus very narrow with inconspicuous sparse short setae, with a sparse row of brown setae overhanging cheliceral bases. Chelicerae brown and robust; posterior margin with single conical tooth. Abdomen a flattened oval, as broad as cephalothorax and indistinctly longer, densely covered by lighter thin adpressed setae. Leg formula: I-IV-III-II; but legs of approximately equal length (leg I longest by about 20%); long and thin, their segments of similar width, with femora somewhat wider, but tibia I not broader than neighboring segment and not shortened (in which it differs from *Pseudicius*). Spines inconspicuous, shorter than sparse upright, reddish setae on the same surfaces; anterior tibia with only ventral spines, on anterolateral edge two short spines located in the anterior one third of seg-
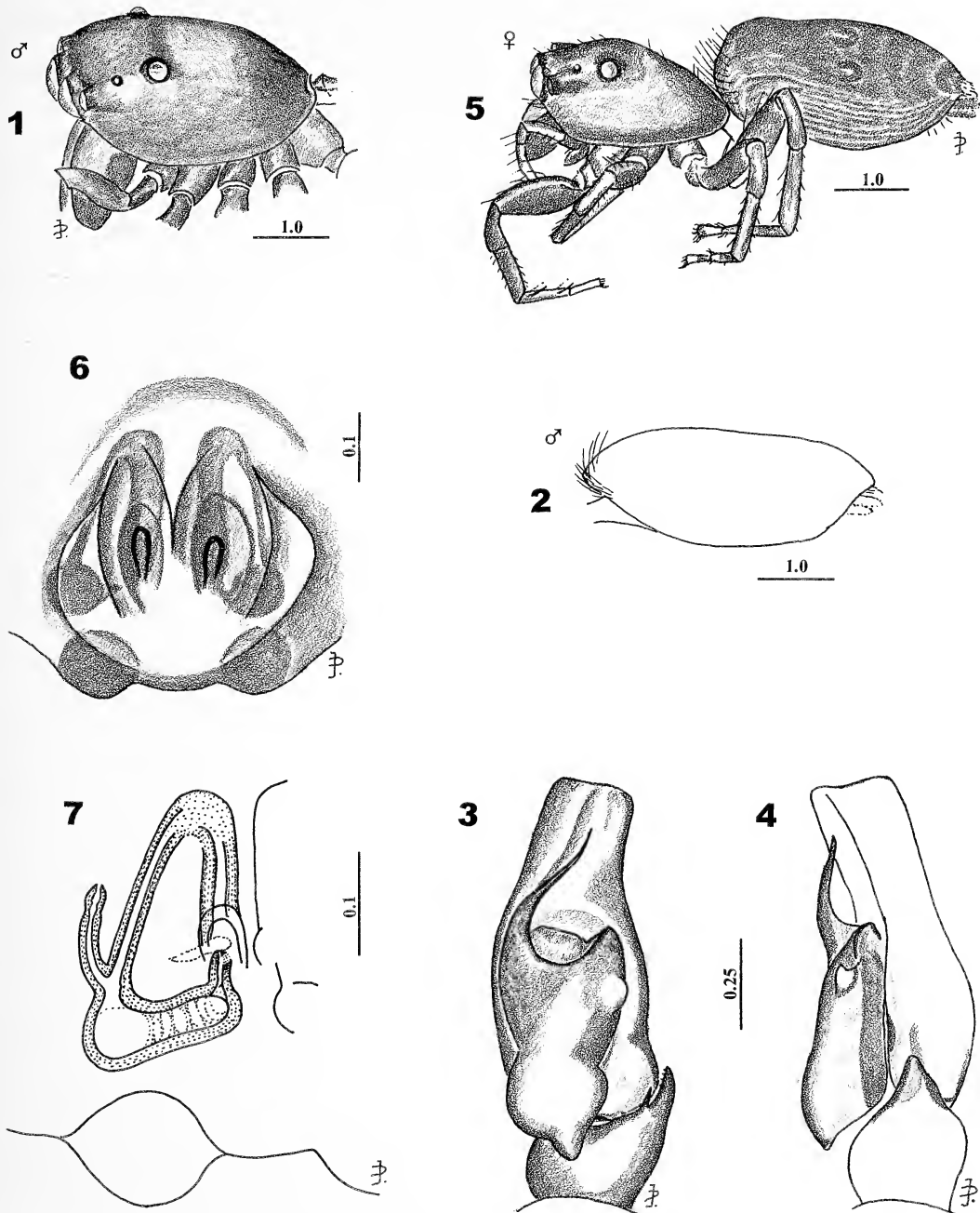
Figures 1–7.—**Hakka himeshimensis** new genus. 1. Male, dorso-lateral view of cephalothorax; 2. Male abdomen, laterally; 3. Palpal organ, ventrally; 4. Palpal organ, laterally; 5. Female, general appearance; 6. Epigynum; 7. Internal structure of epigynum.

ment, on posterolateral edge two short spines, normally spaced. Palpal organ with bulbus broad anteriorly and with anterior margin curved posteriorly (in which it resembles some *Pseudicius* of the *cinctus* group); embolus characteristic, elongate conical with wavy outline.

Female: Resembles male in appearance and size (Fig. 5); difference from male in leg formula (IV-III-II-I) is a secondary sex character,

found in many genera of Salticidae. Characterized by epigynum in a form of a concave plate, with slit-like copulatory openings in the middle, located inside indistinct oval depressions, separated by a thin, low ridge (Fig. 6). Internal structures of epigynum consist of a channel running anteriorly, then curving and running back, slightly diagonal and joining the transversely oriented narrow bag-shaped spermathecae, located in the posterior half of epigynum. There is a long chimney-like structure, presumed to be a scent gland pore (see Prószyński 1998, in press), located at the junction of channel and spermatheca. Walls of channels, spermatheca and scent gland sclerotized and of similar thickness. Interior walls of spermathecae with irregular, transverse ridges. Nutritive pores (see Prószyński 1998, in press) minute and indistinct, located near the top of conical distal part of spermatheca, near insertion of fertilization channel (Fig. 7). General plan and appearance of these structures superficially resemble those seen in various species of *Salticus*.

Distribution.—Japan, China and North Korea; this is the first record from Hawaii.

Material examined.—*Hakka himeshimensis* [*"Pseudicius" himeshimemsis*], under stones, Necker Island, Hawaii, 1♂, 14 June 1923 (E.M. Bryan, Jr., AMNH). *Hakka himeshimensis* [labeled *"Salticus koreanus* (Wesolowska 1981) s. *Pseudicius koreanus"*], on black lava beach, Anaehoomalu Bay, Hawaii County, Hawaii, 1♀, 15 February 1997 (J. & E. Berry). *Hakka himeshimensis* [*"Salticus" koreanus* (Wesolowska 1981) s. *"Pseudicius koreanus"*], among beach rocks near Nailoa, Anaehoomalu beach, Hawaii County, Hawaii, 1♀, 17 February 1988 (J. & E. Berry). All specimens identified by J. Prószyński.

ACKNOWLEDGMENTS

LITERATURE CITED

Bohdanowicz, A. & J. Prószyński. 1987. Systematic studies on East Palaearctic Salticidae (Araneae), IV. Salticidae of Japan. Annales Zoologici, Warszawa 41(2):43–151, figs. 1–312.

Bösenberg, W. & E. Strand. 1906. Japanische Spinnen. Abhanglungen der Senckenbergischen Naturforschenden Gesellschaft 30:93–422, pl. III-XVI.

Chikuni, Y. 1989. Some interesting Japanese spiders of the families Amaurobiidae, Araneidae and Salticidae. Arachnological papers presented to Takeo Yaginuma, Osaka. Pp. 133–152, figs. 1–17.

Peng X., L. Xie & X. Xiao. 1993. Salticidae in China. Hunan Normal Univ. Press. 270 pp. 893 figs. [in Chinese, English summary].

Prószyński, J. 1976. ,Studium systematyczno-zoogeograficzne nad rodzina Salticidae (Aranei) Regionow Palearktycznego i Nearktycznego. Rozprawy Wyzszej Szkoly Pedagogicznej. Siedlce: Pp. 1–260, 450 figs., 218 maps.

Prószyński, J. 1987. Atlas rysunkow diagnostycznych mniej znanych Salticidae 2. Zeszyty Naukowe WSRP, Siedlce, 172 pp., illustr.

Prószyński, J. 1998. Description of new species of *Phlegra* (Salticidae, Araneae) from Israel. Israel Journal of Zoology 44:159–185.

Prószyński, J. In press. Salticidae of the Levant. Fauna Palaestina: Arachnida. The Israel Academy of Sciences and Humanities. Jerusalem.

Wesolowska, W. 1981. Salticidae (Aranei) from North Korea, China and Mongolia. Annales Zoologici (Warszawa) 36:45–83; 112 figs.

Yaginuma, T. 1970. The spider fauna of Japan (revised in 1970). Bulletin of the National Science Museum (Tokyo) 13:639–701.

Yaginuma, T. 1986. Spiders of Japan in Color. (new ed.). Hoikusha Publ. Co., Osaka. Pp. 1–350, figs. 1–135, Plate 65.

A REVISION OF THE AFROTROPICAL SPIDER GENUS *PALFURIA* (ARANEAE, ZODARIIDAE)

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ABSTRACT.   The African genus *Palfuria* Simon 1910 is revised. The genus now contains nine species: the type species *Palfuria retusa* Simon 1910, described on the base of single juvenile, *P. gibbosa* (Lessert 1936), *P. panner* Jocqué 1991, and six species that are described as new: *P. caputlari* (♂♀), *P. harpago* (♂), *P. helichrysorum* (♀), *P. hirsuta* (♀), *P. gladiator* (♂♀), *P. spirembolus* (♂♀). The male of *Palfuria panner* is redescribed, and the female described for the first time. Five species (*P. retusa, P. spirembolus, P. gladiator, P. panner, P. harpago*) are from the southwestern part of the continent, the other species (*P. gibbosa, P. helichrysorum, P. hirsuta, P. caputlari*) from the eastern part. The last species is from as far north as northern Tanzania. As in many other genera, there is a tendency for the embolus to increase in length. Both the most basal (*Palfuria panner*) and the most derived species (*Palfuria spirembolus*) are found in Namibia.

Keywords: Cladistic analysis, complexity, new species

Palfuria is a poorly-known genus, recorded only from the southern part of Africa. Its type species (*Palfuria retusa*) was described on the basis of a single juvenile specimen. Both additional described species (*P. gibbosa* and *P. panner*) were each known from one sex only. Since the revision of Jocqué (1991), an important number of specimens representing several new species has become available. The present paper treating these specimens shows that the diagnostic characters identified by Jocqué (1991) remain valid; but there is a lot of variation in genitalic characters and, to a lesser degree, in somatic traits. Scanning electron micrographs of some important characters are provided, and the distribution of the genus is shown to extend much further north than was known previously.

METHODS

Male right palps were removed, examined and drawn with a Wild M5 stereomicroscope. Epigyna were removed and cleared in methylsalicylate and temporarily mounted in a mixture of that medium and cedukol. They were observed and drawn with a Leitz Dialux 22 compound microscope. Scanning micrographs were made with a JEOL LV 5400 scanning microscope. All measurements are in millimeters.

Abbreviations.—a = diameter of PME, b = diameter of PLE, c = diameter of AME, d = diameter of ALE, e = distance between PME, f = distance between PME and PLE, g = distance between AME, h = distance between AME and ALE. ALE = anterior lateral eyes, AME = anterior median eyes, AW = anterior width (of the MOQ), L = length of the median ocular quadrangle, MOQ = median ocular quadrangle, PLE = posterior lateral eyes, PME = posterior median eyes, PW = posterior width (of the MOQ), PS = posterior spinnerets.

Institutions.—MHNG = Musée d'Historie Naturelle, Genéve (B. Hauser, P. Schwendinger); MNHN = Muséum National d'Histoire Naturelle, Paris (J. Heurtault & C. Rollard); MRAC = Musée Royal de l'Afrique Centrale, Tervuren (R. Jocqué); NMSA = Natal Museum, Pietermaritzburg (P. Croeser, A. Ruiters); NMZ = National Museum Zimbabwe, Bulawayo (M. Fitzpatrick); SMNW = State Museum, Windhoek, Namibia (E. Griffin).

TAXONOMY

Palfuria Simon 1910

Palfuria Simon 1910: 188 (description new genus). Jocqué 1987: 143; 1991: 141.
Dippenaar Schoeman & Jocqué 1997: 327.

Hermippella Lessert 1936: 226 (description new genus); 1938: 432 (formerly included in the *Palpimanidae*).

Note: Jocqué (1991) provisonally synonymized *Palfuria* and *Hermippella;* this synonymy can now be considered as definitive. It is indeed found that in juveniles, and even in some females, that the cephalic lobe is only raised and not slanting back as in *Palfuria retusa.*

Type species.—*Palfuria retusa* Simon 1910.

Diagnosis.—Easily recognized by the strongly elevated cephalic part of the carapace, slanting back in adults (except *P. spirembolus* female); the abdomen has dorsolateral circumferential folds. The genus is part of a large unresolved clade (Jocqué 1991) of genera with a femoral organ but the characters listed above unequivocally distinguish *Palfuria* from them. *Heradida* Simon 1893 is the only genus in that clade with abdominal circumferential folds and must be considered the sister-group of *Palfuria.*

Description.—(slightly modified after Jocqué 1991: 141–142.) Small spiders (1.41–3.4) with slightly to strongly granulated tegument. Carapace with strongly raised cephalic lobe, slanting back over the thoracic area in adults; widest between coxae III and IV; narrowed in front to about 0.75× maximum width in females, to about 0.65× maximum width in males. *Color:* Carapace and chelicerae pale to dark brown. Sternum pale yellow to dark brown, often with a darker margin. Legs dark brown to a pale yellow, sometimes with dark stripes; coxae and trochanters pale yellow, femora slightly darker, other leg segments paler. Abdomen pale to dark sepia on dorsum, pale on sides and venter. *Eyes:* In two strongly procurved rows (anterior one as seen in front, posterior one as seen from above). AME by far the largest up to 4× diameter of other eyes), dark (except *P. spirembolus*), circular. Other eyes pale, circular, though PME sometimes slightly ovoid. AME about half their diameter apart, about one diameter from

PLE; these almost contiguous with ALE and AME. MOQ subquadrangular. *Clypeus:* Convex, high 3.5–10× as high as diameter of ALE. Chilum absent. *Chelicerae:* Short, fused; without lateral condyle; without teeth, but with cheliceral lamina (Fig. 4). Interchceliceral triangle most often small. Endites roughly rectangular, strongly converging; with anteromesal scopula. Labium triangular. Sternum as wide as long in females, longer than wide, slightly rebordered in males. *Legs:* Formula 4123. More slender in males than in females. Two claws on short onychium; with 2–4 teeth, third claw tiny; no claw tufts but spiniform scopulae present. One dorsal spine in proximal half of femora. Leg segments generally covered with flattened incised hairs (Figs. 1, 2), but femora with 2–4 long rigid hairs, (for example: in *P. gladiator, P. hirsuta*). Femoral organ with 1 or 2 barbed hairs (Fig. 1). Patellae with proximal ring-shaped crack (see Jocqué & Dippenaar-Schoeman 1992, fig. 5). *Abdomen:* Rounded, hardly longer than wide; slightly sclerotized on dorsum in females, more strongly so in males; anterior part of abdomen strongly sclerotized, forming tube around the petiolus; with a number of parallel shallow, circumferential folds. Two spinnerets in males, 4 spinnerets in females, PS minute. Colulus represented by broad field with short setae; a number of modified hairs in front of tracheal spiracle (Fig. 3); spiracle wide with anterior rim sclerotized. *Male palp:* (Figs. 5–15): Tibia with one or two slender lateral apophyses. Cymbium with distal filed of short hairs and one or two dorsolateral modified hairs. Embolus originating on posterior part of tegulum (except *P. spirembolus*), curved, relatively short. Tegular apophysis fairly short, sometimes bifurcate. *Female palpus:* With finely pectinated claw. *Epigynum:* (Figs. 16–29) Very simple to relatively complex, poorly sclerotized except in *P. helichrysorum.*

Distribution.—Africa south of 4°S: found in Tanzania, Namibia, Malawi, Zambia, Mozambique, South Africa.

KEY TO THE SPECIES

Note: Palfuria retusa Simon is not included since it is known only from the juvenile.

1. Males 2
   Females 6
2. Embolus long, looped around the tegulum (Figs. 14, 15) . . . . *Palfuria spirembolus*
   Embolus very short (Figs. 5–10, 12, 13) 3
3. Palpal tibia with two apophyses, one dorsal,
   one retrolateral (Figs. 6, 10–11) 4
   Palpal tibia with only one apophysis (Figs. 8, 13) 5
4. Dorsal apophysis almost straight (Fig. 6) . . . .*Palfuria caputlari*
   Dorsal apophysis harpoon shaped; slightly curved, pointed, with a branch pointing backwards,
   ending in a few fine, hair like ramifications (Figs. 10, 11) . . . . *Palfuria harpago*
5. Tibial apophysis straight (Fig. 8) . . . .*Palfuria gladiator*
   Tibial apophysis curved (Fig. 13) . . . . *Palfuria panner*
6. Epigynum with well delimited plate (Figs. 16, 17, 19, 20) 7
   Epigynum without a plate, but with sclerotized posterior margin (Figs. 18, 21, 22) 10
7. Epigynal plate of different shape, with posterior margin sinuous and indented in the middle (Fig.
   19) . . . .*Palfuria helichrysorum*
   Epigynal plate ellipsoid (Figs. 16, 17, 20) 8
8. Entrance openings situated near posterior margin of epigynum. Spermathecae under plate, lateral
   margins of epigynum plate angular (Fig. 17) . . . .*Palfuria gibbosa*
   Entrance openings—if visible—nearer to anterior margin of the epigynum; spermathecae at var-
   iable distance from epigynal plate, but never under it. Lateral margins of epigynum plate evenly
   rounded (Figs. 16, 20) 9
9. Internal structure of epigynum relatively complex, sperm ducts long and wound (Fig. 27) . . . . .
   . . . .*Palfuria hirsuta*
   Internal structure of epigynum simple, sperm ducts short and slightly curved (Fig. 23) . . . .
   . . . .*Palfuria caputlari*
10. Epigynum with only a simple, small, sclerotized posterior margin (Fig. 18) . . . . .*Palfuria gladiator*
    Epigynum with differently shaped sclerotized parts 11
11. Sclerotized margin of the epigynum straight, situated posteriorly, spermathecae rounded; atria
    large (Figs. 21, 28) . . . . *Palfuria panner*
    Posterior margin of epigynum accolade shaped, spermathecae oval; atria small, glandular organ
    present (Figs. 22, 29) . . . . *Palfuria spirembolus*

Palfuria caputlari new species
Figs. 1–6, 16, 23, 30, 31

Holotype.—Male, Tanzania, Mkomazi Game Res., Ibaya camp, Nov. 1994, Russell-Smith (MRAC 202.528).

Paratypes.—3♀14♂ together with holo-type.

Diagnosis.—Males of *Palfuria caputlari* are easily identified by the long, slender dorsolateral tibial apophysis of the palp and the hook-shaped median apophysis (Figs. 5–6). Females are recognized by the epigynal plate which is much wider than long (length/width 0.3) (Fig. 16). The male shows superficial resemblance with *P. harpago* with which it shares the presence of two tibial apophyses; in the latter species the dorsolateral apophysis is harpoon-shaped; the female is similar to *P. hirsuta* but lacks the long entrance ducts of

that species. The sister-species of *P. caputlari* is *P. harpago*.

Etymology.—The species name is composed of two Latin nouns: *caput* (head) and *lari* (gen. of *Larus:* gull), referring to the shape of the median apophysis as seen from the side.

Male.—Total length 2.24 (2.24–2.35); carapace 1.12 long (1.12–1.32), 0.82 wide (0.77–0.91). *Color:* Carapace medium to dark brown, with some faint, darker striae in thoracic area. Cephalic lobe dark brown, with some paler spots. Eye field dark brown. Chelicerae medium brown, fangs yellow, cheliceral lamina white, sternum medium brown, sometimes with dark margin; legs paler: coxae pale yellow, femora dark brown, other leg segments pale yellow. Abdomen: dorsum dark sepia with yellow folds, contrasting with pale yellow venter. Branchial operculum dark yel-
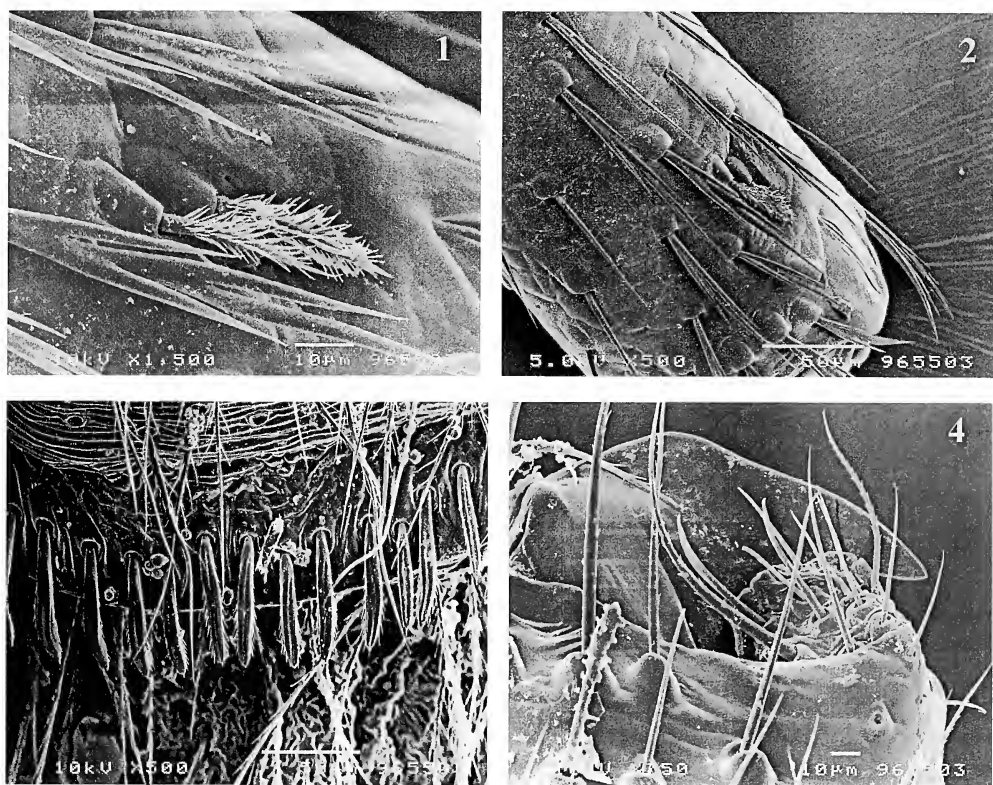
Figures 1–4.—*Palfuria caputlari,* male from Mkomazi Game Reserve. 1, Femoral organ, leg I; 2, Position of femoral organ on right femur I; 3, Modified hairs in front of spinnerets; 4, Cheliceral lamina.

low. *Carapace:* (Figs. 30, 31): Tegument slightly granulated. *Chelicerae:* setae of cheliceral lamina curved, subequal. *Abdomen:* Circumferential folds not conspicuous, modified hairs in front of spinnerets stout. *Eyes:* a: 0.06; b: 0.06; c: 0.13; d: 0.06; e: 0.13; f: 0.14; g: 0.05; h: 0.04; MOQ: AW = 1.35 PW; AW = 1.25 L. Clypeus: 0.39 or 6.5× diameter of ALE. *Legs:* All segments covered by flattened incised hairs. Two dorsal spines and three long ventral rigid hairs on all femora. *Male palp:* (Figs. 5, 6). Tibia with two apophyses; one dorsal, one retrolateral; dorsal apophysis long, thin, almost straight; retrolateral apophysis medium sized, wider; median apophysis pointed, hook shaped; embolus short, blunt.

Female.—Total length 2.44 (2.31–2.44); carapace 1.42 long (1.22–1.42), 1.02 wide (0.91–1.02). *Color:* Carapace medium to dark brown, with some darker striae in thoracic area. Cephalic lobe dark brown, with some paler spots. Chelicerae medium brown, fangs yellow, cheliceral lamina white, sternum pale brown, with dark margin, legs paler: coxae

pale yellow, femora dark brown, paler on the ventral side, other leg segments pale yellow. Abdomen: dorsum dark sepia with yellow folds, contrasting with pale yellow venter. Branchial operculum dark yellow. *Carapace:* Hair cover slightly denser than in males. *Abdomen:* Circumferential folds poorly marked, modified hairs in front of spinnerets stout. *Epigynum:* (Figs. 16, 23). With narrow plate, with dark posterior margin; internal structure of epigynum simple: sperm ducts short, almost straight, spermathecae rounded.

Distribution.—Only known from type locality.
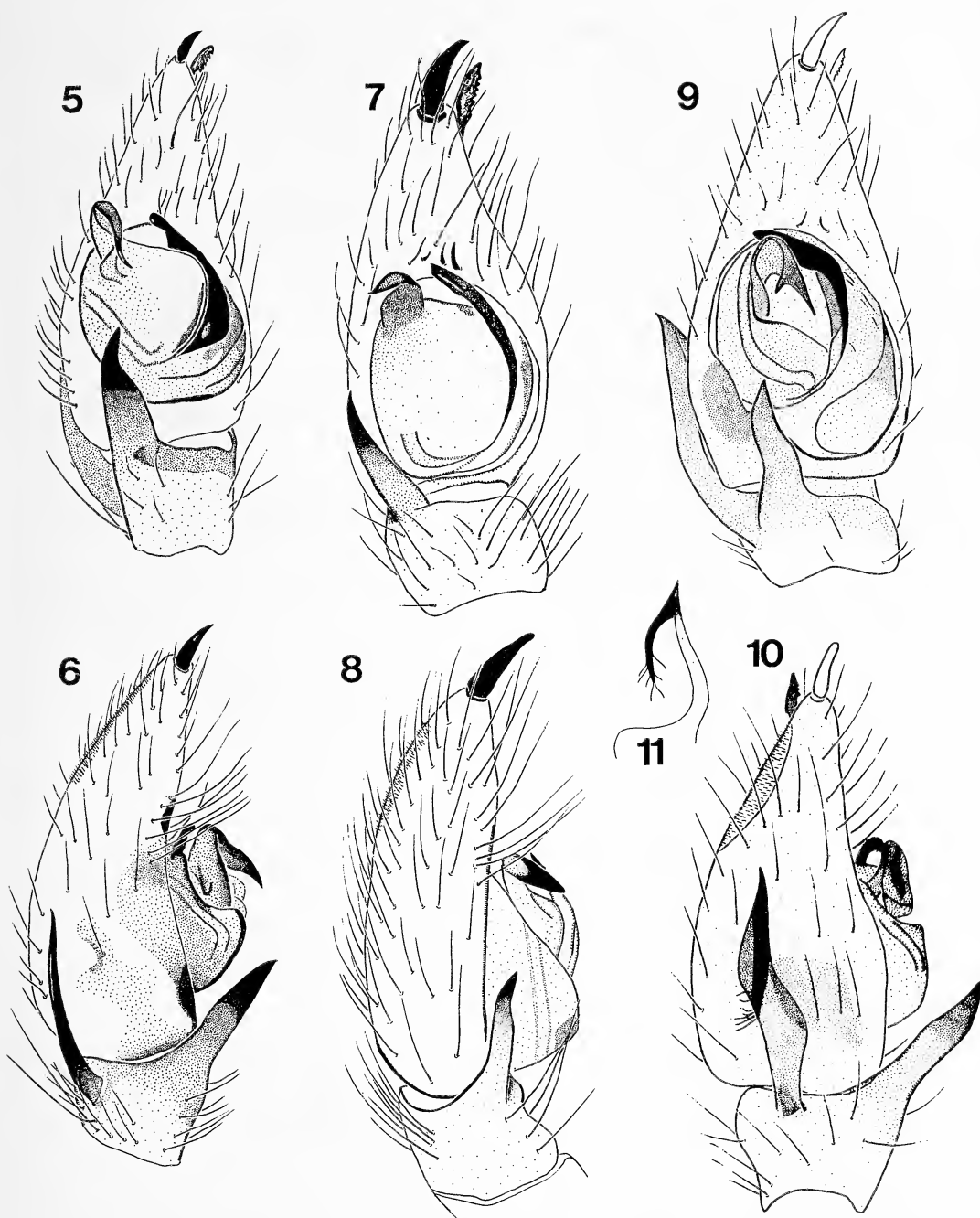
Palfuria gibbosa (Lessert)
Figs. 17, 24

Hermippella gibbosa Lessert 1936: 226 (description female); 1938: 432.
Palfuria gibbosa: Jocqué 1991: 142.

Holotype.—Female, Mozambique, Nova Choupanga (? near Chupanga 18°05′S, 35°35′E) (MHNG) (examined).

**Diagnosis.**—The females of *Palfuria gib-*

Figures 5–11.—Male palps. 5, 6. *Palfuria caputlari* from Mkomazi Game Reserve. 5, Ventral view; 6, Retrolateral view. 7, 8. *P. gladiator,* holotype. 7, Ventral view; 8, Retrolateral view. 9–11. *P. harpago,* holotype; 9, Ventral view; 10, Retrolateral view; 11, Detail of dorsolateral apophysis, dorsal view.

bosa can be recognized by the shape of the epigynal plate, the entrance openings near the posterior margin of the plate and the presence of glands. The epigynum vaguely resembles that of *P. helichrysorum* but lacks the poste-rior median indentation; the epigynal plates of *P. caputlari* and *P. hirsuta* both have rounded lateral margins and a sclerotized posterior rim. The closest relatives of *P. gibbosa* are *P. spi-rembolus* and *P. hirsuta.*
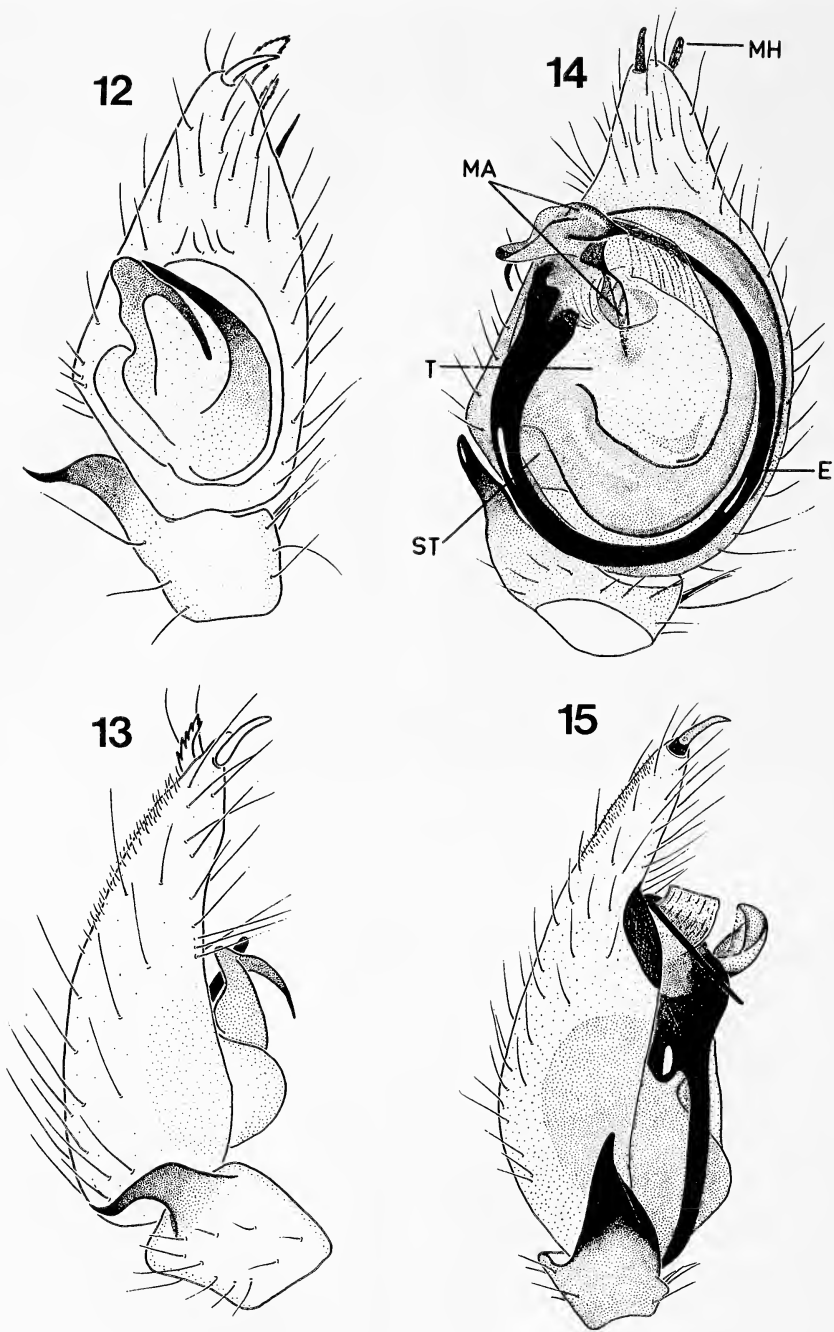
Figures 12–15.—Male palps. 12, 13. *Palfuria panner,* SMNW42872; 12, Ventral view; 13, Retrolateral view; 14, 15. *P. spirembolus,* holotype; 14, Ventral view; 15, Retrolateral view. (E = embolus; MA = median apophysis; MH = modified hair; ST = subtegulum; T = tegulum).

Female.—Total length 2.30, carapace 1.10 long, 0.64 wide. *Color:* Carapace medium brown in cephalic area, pale brown in thoracic area; chelicerae medium brown. Sternum yellow. Legs pale yellow. Abdomen greyish-yellow on sides and venter. *Carapace:* (see Jocqué, 1991 figs. 354–356). With raised cephalic lobe slanting back over thoracic area. *Eyes:* a: 0.06; b: 0.06; c: 0.1; d: 0.08; e: 0.12; f: 0.07; g: 0.06; h: 0.03. MOQ: AW = 1.04
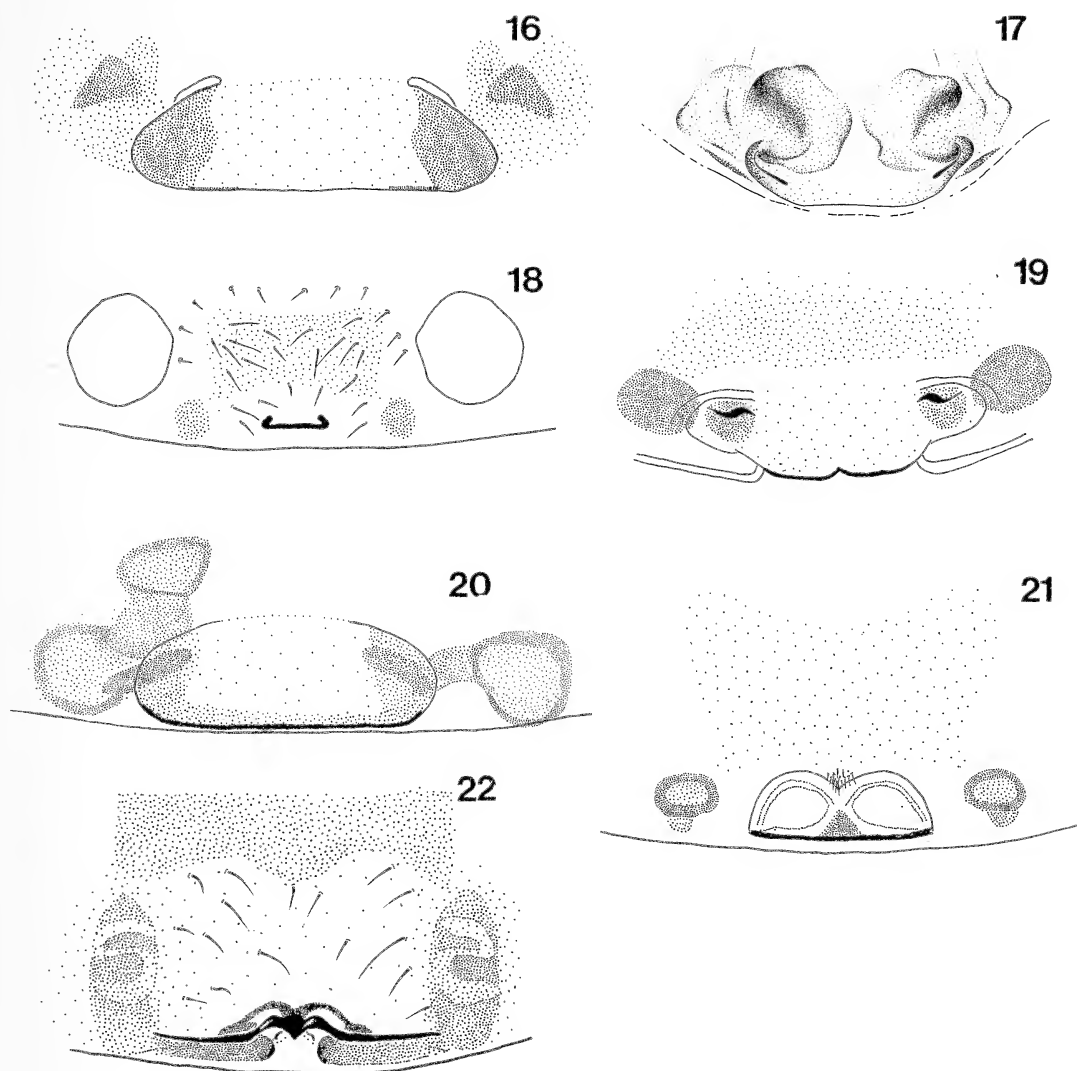
Figures 16–22.—Epigyna, ventral view. 16, *Palfuria caputlari* from Mkomazi Game Reserve; 17, *P. gibbosa,* holotype; 18, *P. gladiator,* paratype; 19, *P. helichrysorum,* holotype; 20, *P. hirsuta,* holotype; 21, *P. panner* from Windhoek; 22, *P. spirembolus* from Kokerboom forest.

PW; AW = 1.00 L. *Legs:* only leg II complete. *Epigynum:* (Figs. 7, 24). Entrance openings situated near posterior margin, spermathecae under epigynal plate, provided with angular lateral margin.

Male.—Unknown.

Distribution.—Only known from type locality.

Palfuria gladiator new species
Figs. 7, 8, 18, 25

Holotype.—Male, Namibia, Karossfontein 19°21′S, 14°31′E, 7 Oct.–14 Nov. 1986, pitfall traps, E. Griffin (SMNW 39751).

Paratypes.—Namibia: 2♂ together with holotype; ♂ from Windhoek, wasteland near houses, 14–31 Oct. 1987 pitfall traps, R. Jocqué (MRAC 168.421); 6♂ 1♀ from Damaraland, Hobatere Campsite, 19°8′S, 14°7′E, 23–30 April 1996, pitfall traps, E. Griffin (SMNW 43540; 1♂ in MRAC); ♂ and ♀ from Hobatere Campsite, 3.2 km from gate, 19°9′S, 14°7′E, 7–17 May 1991, pitfall traps (SMNW 42632); ♀ from Wolfsnes, 19°03′S, 15°52′E, 24 March–10 May 1988, pitfall traps, E. Griffin (SMNW 40890).

Diagnosis.—Representatives of this species can be recognized by the strongly granulated
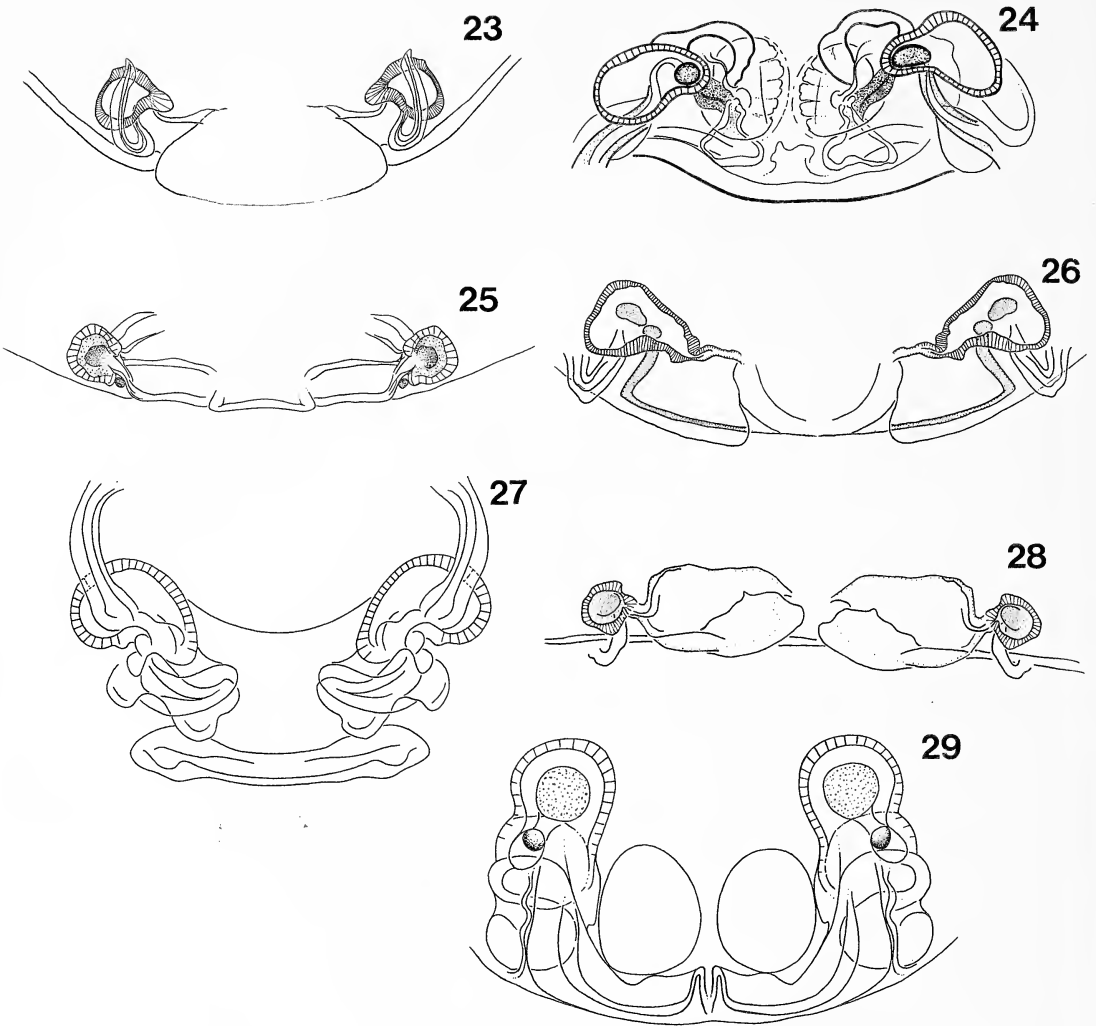
Figures 23–29.—Epigyna, cleared, dorsal view. 23, *Palfuria caputlari* from Mkomazi Game Reserve; 24, *P. gibbosa,* holotype; 25, *P. gladiator,* paratype; 26, *P. helichrysorum,* holotype; 27, *P. hirsuta,* holotype; 28, *P. panner* from Windhoek; 29, *P. spirembolus* from Kokerboom forest.

tegument of the carapace and by the two (one dorsal, one ventral) long, rigid hairs on tibia II-III. Males of *Palfuria gladiator* are characterized by the big cymbial claw and the almost straight palpal tibial apophysis. The females can easily be identified by the epigynum, appearing as a short, sclerotized, transverse line. Males and females are superficially similar to those of *P. panner,* the closest relative, but in that species the male palpal tibial apophysis is turned upwards and in the female there is a slight depression in front of the sclerotized epigynal rim.

Etymology.—The species name is a noun in apposition and refers the shape of the male carapace and the big tarsal claw on the male palp.

Male.—Total length 2.04 (1.41–2.04); carapace 1.06 (0.75–1.06) long, 0.71 (0.56–0.71) wide. *Color:* Carapace dark brown; cephalic area much darker, thoracic area paler, with some darker striae, cephalic lobe of carapace dark brown, lateral part of carapace paler, contrasting with dark top. Chelicerae brown, fangs yellow, cheliceral lamina poorly developed, sternum pale yellow with dark margin; legs paler: coxae pale yellow, femora I-II dark brown, femora III-IV dark brown on dorsal side, paler on ventral side, tibiae dark yellow, other leg segments pale yellow. Abdomen

dorsum dark sepia with paler folds, venter pale yellow, with contrasting boundary between them on sides. Branchial operculum pale brown. *Carapace:* Tegument strongly granulated. *Chelicerae:* Setae on cheliceral lamina small, poorly developed in males. Base of fangs strongly granulated, with long setae. Sternum: with many, fine hairs. *Abdomen:* Dorsum with some strong hairs. Modified hairs in front of spinnerets strong. *Eyes:* a: 0.05; b: 0.05; c: 0.11; d: 0.07; e: 0.12; f: 0.10; g: 0.04; h: 0.01; MOQ: AW = 1.18 PW; AW = 1.04 L. *Clypeus:* 0.3 or 4.2× diameter of ALE. *Legs:* All segments covered with flattened incised hairs. One dorsal spine, three ventral rigid hairs on all femora, one dorsal, one ventral rigid hair on tibia II-III. *Male palp:* (Figs. 7, 8). Tibia with one almost straight; medium sized prolateral apophysis; median apophysis pointed, hook-shaped; embolus long, blunt.

Female.—Total length 2.47 (2.04–2.27); carapace 1.03 long (0.9–1.03), 0.92 wide (0.75–0.92). *Color:* Carapace dark brown, with some darker striae in thoracic area, which paler. Cephalic lobe dark brown. Chelicerae brown, fangs yellow, cheliceral lamina white; sternum pale brown, with dark margin; legs paler: coxae pale yellow, femora dark brown, paler on ventral side, other leg segments pale yellow. Abdomen: dorsum dark sepia with yellow folds, contrasting with pale yellow venter. Branchial operculum dark yellow. *Carapace:* Hair cover slightly denser than in males. *Abdomen:* Circumferential folds not conspicuous; some stout modified hairs in front of the spinnerets. *Epigynum:* (Figs. 18, 25). Simple; with short, transverse sclerotized line. Internal structure of epigynum similar to that of *Palfuria panner,* but fertilization ducts turned upward.

Distribution. Known only from Namibia.

Palfuria harpago new species
Figs. 9–11

Holotype.—Male, Namibia, Ovamboland, 10 km SE Etunda, 17°26′S, 14°33′E, 20 July–9 August 1989, pitfall traps, E. Marais (SMNW 41413).

Paratype.—1♂ from Namibia, Ovambo, Mahanene Agric. Res. Sta., 17°26′S, 14°47′E, 5 October–5 December 1993, pitfall traps, B. Wohlleber (SMNW 43396).

Diagnosis.—Males of *Palfuria harpago* are easily identified by the shape of the dorsolateral tibial apophysis: almost straight, pointed and with a branch pointing backwards, ending in a few, fine hair-like ramifications. *Palfuria caputlari* is the only other *Palfuria* with two palpal tibial apophyses; in *P. caputlari,* however, the dorsal one is long, straight and spine-shaped. The sister-species of *P. harpago* is *P. caputlari.*

Etymology.—The species name is a noun in apposition (*harpago,* Latin for harpoon) referring to the shape of the dorsal tibial apophysis as seen from the dorsolateral side (Fig. 11).

Male.—Total length 1.81 (1.81–1.98); carapace 1.13 long (1.03–1.22), 0.92 (0.66–0.92) wide. *Color:* Carapace medium to dark brown, with some faint, darker striae in thoracic area. Cephalic lobe pale brown with dark margin. Eye field dark brown. Chelicerae medium brown, fangs dark brown, cheliceral lamina white; sternum pale brown, without darker margin; legs pale brown or yellow. Abdomen: dorsum shiny, dark sepia with pale circumferential folds, venter dark yellow, contrasting with dark sides. Branchial operculum dark yellow. *Carapace:* Tegument slightly granulated on cephalic lobe. *Chelicerae:* Setae of cheliceral lamina curved, and subequal. *Abdomen:* Modified hairs in front of spinnerets fine and long, but few. Ventral side of abdomen with many hairs. *Eyes:* a: 0.05; b: 0.05; c: 0.11; d: 0.09; e: 0.19; f: 0.05; g: 0.04; h: 0.02; MOQ: AW = 1.18 PW, AW = 1.36 L. Clypeus: 0.32 or 3.5× diameter of ALE. *Legs:* All segments covered with flattened incised hairs. Femora with one dorsal spine and cover of ordinary hairs. *Male palp:* (Figs. 9, 10). Tibia with two apophyses; one ventral, one dorsolateral. Ventral apophysis short and wide, slightly curved, dorsolateral apophysis long, pointed, harpoon-shaped, with back-pointing branch ending in few thin ramifications. Median apophysis strongly curved, bifid, ending in two pointed tips; embolus short, wide, subtegulum present, hidden under cymbium.

Female.—Unknown.

Distribution.—Only known from Ovamboland, Namibia.

Palfuria helichrysorum new species
Figs. 19, 26

Holotype.—Female, Malawi, Mt. Mulanje, Lichenya plateau (2000 m), near CCAP hut,

15°59′S, 35°32′E, 9 November 1981, under *Helichrysum,* R. Jocqué (MRAC 156.781).

Diagnosis.—*Palfuria helichrysorum* females are recognized by the sclerotized epigynum and the shape of the central plate with two frontal lobes covering the entrance openings, and indented posterior margin, and by the internal structure of the epigynum with short, thick-walled sperm ducts. The other species with an epigynal plate, *P. caputlari, P. gibbosa* and *P. hirsuta* lack the posterior indentation. *P. helichrysorum* is the sister-taxon of a group of three species comprising *P. hirsuta, P. spirembolus* and *P. gibbosa.*

Etymology.—The specific name is derived from *Helichrysum,* a rosette bearing Asteraceae, ideal retreat for night active spiders.

Female.—Total length 3.06; carapace 1.32 long 0.98 wide. *Color:* Carapace dark brown, with some darker striae in thoracic area. Cephalic lobe dark. Chelicerae brown, fangs yellow, cheliceral lamina white, sternum pale brown, with wide, dark margin; legs paler: coxae yellow, femora dark brown, femora I-II paler on ventral side, other leg segments pale yellow, contrasting with dark femora. Abdomen: dorsum dark sepia with yellow, circumferential folds; venter pale yellow, contrasting with dark sides. Branchial operculum brown. *Carapace:* Finely granulated. *Chelicerae:* Setae of cheliceral lamina straight, unequal in length. *Abdomen:* Dorsum with few fine hairs. Modified hairs in front of spinnerets fine. Eyes: a: 0.07; b: 0.07; c: 0.12; d: 0.07; e: 0.16; f: 0.08; g: 0.08; h: 0.08; MOQ: AW = 1.06 PW; AW = 1.15 L. *Clypeus:* 0.34–4.8× diameter of ALE. *Legs:* Covered with flattened incised hairs. Femora with one dorsal spine and three long ventral rigid hairs. *Epigynum:* (Figs. 19, 26). Well-sclerotized; central plate with two anterior lobes covering entrance openings, posterior margin indented. Internal structure of epigynum quite simple with short, thick walled sperm ducts.

Male.—Unknown.

Distribution.—Only known from type locality.

Palfuria hirsuta new species
Figs. 20, 27

Holotype.—Female, Zambia, Wildlives Game Farm, 16°52′S, 26°37′E, B.F.A. Study Plot, 8–14 Dec. 1994, F. Nyathi (NMZ/A11862).

Diagnosis.—The female of *Palfuria hirsuta* is recognized by the large epignyal plate with clearly sclerotized posterior rim, and the internal structure of the epigynum with long and winding sperm ducts, but lacking a glandular organ. In the other species with an epigynal plate the shape is clearly different (*P. gibbosa; P. helichrysorum*) or the entrance ducts are much shorter (*P. caputlari*). *Palfuria hirsuta* is the sister species of *P. spirembolus* and *P. gibbosa.*

Etymology.—The species name refers to the hairy appearance.

Female.—Total length 2.32; carapace 1.16 long, 0.85 wide. *Color:* Carapace brown; cephalic area dark, thoracic area paler, with some faint darker striae, cephalic lobe very dark. Chelicerae dark brown, fangs yellow, cheliceral lamina white, sternum yellow, with dark margin, anterior part of sternum darker; legs darker: coxae yellow, femora brown with darker sides, other leg segments slightly paler. Abdomen: sepia on dorsum, with yellow folds, pale yellow on venter, but dorsal dark area narrow. Pale spots on sepia background rounded or irregular. *Carapace:* Slightly granulated, with many fine hairs. *Chelicerae:* lamina with two straight setae of different length. *Sternum:* Sternum with fine hairs on anterior—darker—part. *Abdomen:* Dorsum with many fine hairs. Modified hairs in front of spinnerets strong. *Eyes:* a: 0.06; b: 0.07; c: 0.1; d: 0.06; e: 0.06; f: 0.08; g: 0.07; h: 0.04; MOQ: AW = 1.17 PW; AW = 0.96 L. *Clypeus:* 0.35–5.8× diameter of ALE. Legs: Segments covered with flattened incised hairs, but femora, patella, tibia with many rigid hairs. *Leg spination:* One dorsal spine on all femora, long rigid hairs on femora, patella, tibia, but none on tarsi, metatarsi. *Epigynum:* (Figs. 20, 27). With simple ellipsoid plate. Internal structure of epigynum complex: sperm ducts long and intricately wound.
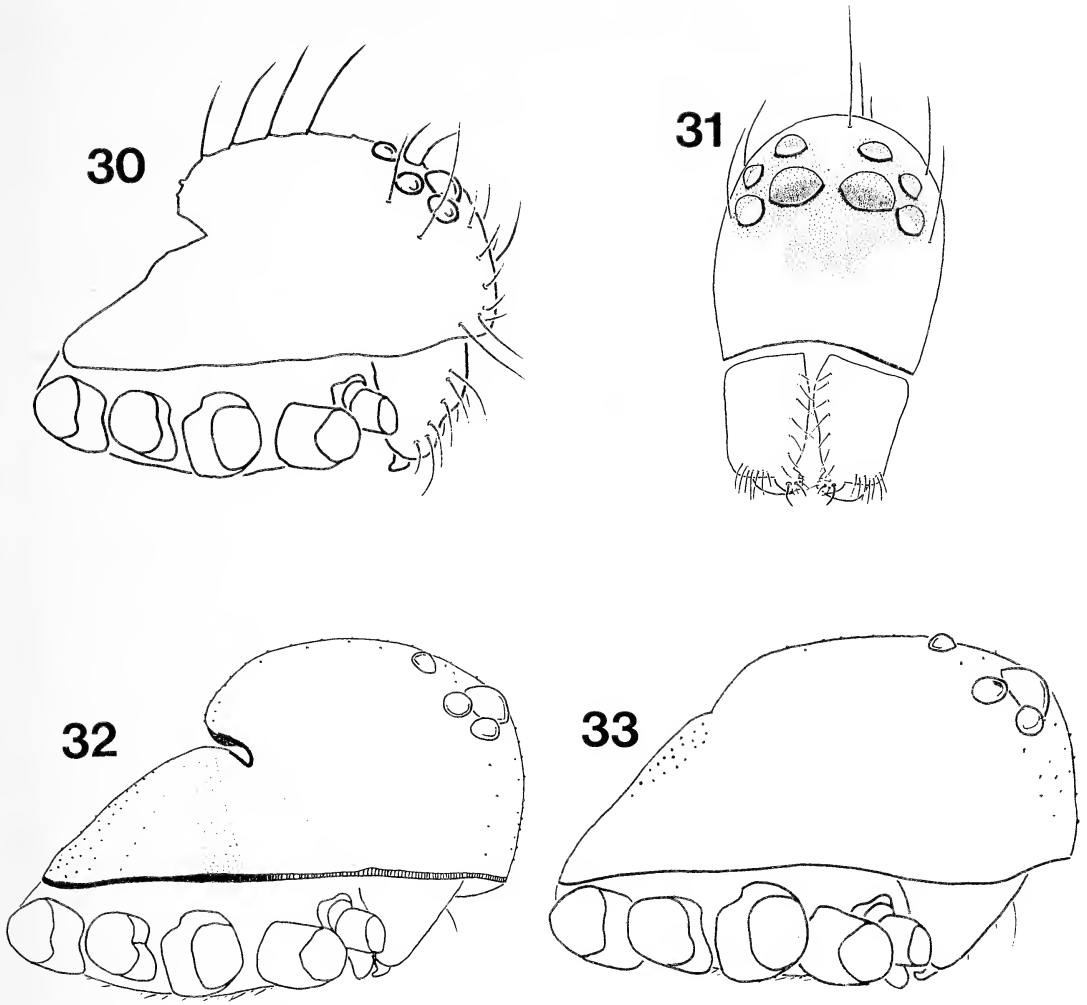
Male.—Unknown.

Distribution.—Only known from type locality.

Palfuria panner Jocqué
Figs. 12, 13, 21, 28

Palfuria panner Jocqué 1991: 142 (description male, figs. 359–363).

Holotype.—Male, Namibia, Panner Gorge, 22°19′S 15°01′E, 11 March–9 April 1985, J. Irish and H. Rust (SMN 38730).

Figures 30–33.—Carapace. 30, 31. *Palfuria caputlari,* male from Mkomazi Game Reserve. 30, Carapace, lateral view; 31, Frontal view. 32, 33. *Palfuria spirembolus* from Kokerboom forest. 32, Male carapace, lateral view; 33, Female carapace, lateral view.

Other material examined.—NAMIBIA:1♂ from Otjiwarongo district, Waterberg Plateau Park, 20°24′S, 17°23′E, 18 May–24 April 1991, pitfall traps, M. Push (SMNW 42465); 1♂ from sand dunes east of Jakkalsputz, SE 2214 Ab, 17–23 April, pitfall traps, 1994, E. Griffin (SMNW 43229); 1♂ from Windhoek district, Richthofen 126, 22°15′S, 17°30′E, 1–31 Oct. 1979, pitfall traps, M.-L. Pentith (SMNW 42872); 1♀ from Windhoek, in trunks and leaves of dead Aloe, 15 Oct. 1987, R. Jocqué (MRAC 168.482); 1♀ from Fransfontein 2015 AA, 22. Feb. 1969, B. Lamoral & R. Day (NMSA); 1 subadult ♂ from Lüderitz district, 29°59′S, 16°14′E, 22 Nov. 1995, under stones, E. Griffin (SMNW 43479).

Diagnosis.—Males of *Palfuria panner* can be recognized by the upward curved palpal tibial apophysis (Fig. 13) and simple fairly long median apophysis. The females can be recognized by the shape of the shallow epigynal depression in front of a sclerotized ridge and the large atria in the epigynum (Fig. 28). The only other species with a simple retrolateral tibial apophysis is *P. gladiator,* but in that species the tibial apophysis is almost straight. The female of *P. gladiator* has a sclerotized line but lacks the depression in front of it. *Palfuria panner* is closely related to *P. gladiator.*

Note: In the holotype, the tip of the tibial apophysis is broken off; the drawing in Jocqué (1991, fig. 361) does not give the normal shape of this apophysis which is here corrected.
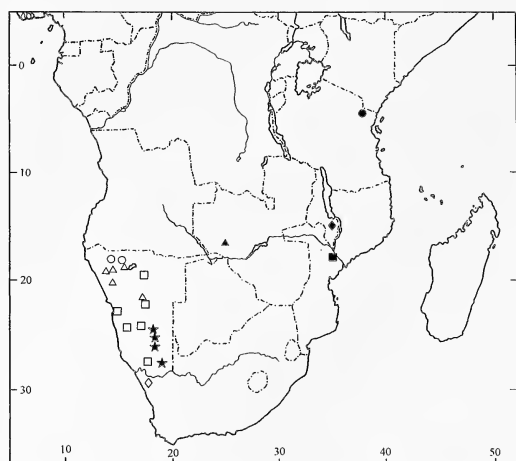
Figure 34.—Distribution map of *Palfuria* species. ● = *P. caputlari;* ■ = *P. gibbosa;* △ = *P. gladiator;* ○ = *P. harpago;* ♦ = *P. helichrysorum;* ▲ = *P. hirsuta;* □ *P. panner;* ◊ = *P. retusa;* ★ = *P. spirembolus.*

Male.—Total length 1.82 (1.69–2.0); carapace 0.90 (0.73–0.98) long, 0.64 (0.58–0.64) wide. *Color:* Carapace dark brown in cephalic area, medium brown with darker striae in thoracic area cephalic lobe pale brown, with some pale spots. Eye field darker. Chelicerae medium brown; sternum shiny dark brown; legs dark brown. Abdomen sepia on dorsum and sides, pale yellow on venter. Branchial operculum medium brown. *Carapace:* Slightly granulated. Cephalic lobe low. *Abdomen:* Circumferential folds well developed. Modified hairs in front of spinnerets stout. *Eyes:* a: 0.05; b: 0.06; c: 0.09; d: 0.05; e: 0.10; f: 0.04; g: 0.05; h: 0.01; MOQ: AW = 1.09 PW; AW: 1.00 L. *Clypeus:* 0.26–5.2× diameter of ALE. *Legs:* Segments covered with flattened incised hairs. Femora with one dorsal spine and three ventral, rigid hairs; tibiae with one ventral rigid. *Male palp:* (Figs. 12, 13). Cymbium with two modified hairs and one spine. Tibial apophysis curved upward. Median apophysis pointing inward, hook shaped.

Female.—Total length 2.23; carapace 1.28 long, 0.92 wide. *Color:* Carapace brown; cephalic area darker, thoracic area pale, with some dark striae. Chelicerae brown, fangs yellow, cheliceral lamina white, sternum yellow with narrow dark margin; legs paler: coxae yellow; femora dark brown, patellae yellow, tibiae dark yellow, with few brown rings, other leg segments much paler. Abdomen: dor-

sum dark sepia with yellow stripes, venter paler, contrasting with darker sides. Branchial operculum pale brown. *Carapace:* Tegument slightly granulated. Cheliceral lamina with two hairs; one stout, short, one finer and longer. Sternum with fine hairs. *Abdomen:* Dorsum with few stout hairs. Modified hairs in front of spinnerets stout and strong. *Epigynum:* (Figs. 21, 28) With sclerotized margin. Incurved, anterior edge with many, fine hairs. Internal structure: openings funnel-shaped, sperm ducts short, spermathecae thick-walled. Fertilization ducts curved downwards.

Distribution.—Only known from Namibia.

Palfuria retusa Simon

Palfuria retusa Simon 1910: 188 (description juv. female); Jocqué 1991: 142 (figs. 352, 353).

Holotype.—Juvenile female, South Africa, Namaqualand, Steinkopf, Shultze (MNHN 1573) (not examined).

Diagnosis.—Recognized by the dark stripes on the femora. Since this species is only known from a juvenile it is not possible to discuss its affinities.

Subadult female.—Total length: 1.98; carapace 1.00 long, 0.72 wide. *Color:* Carapace pale brown with dark margin. Chelicerae pale brown, sternum pale yellow, legs pale yellow: femora with dark stripes. Abdomen dorsum pale sepia with pale stripes in back, remainder cream. *Carapace:* Finely granulated; cephalic area raised, but not slanting back. *Abdomen:* Almost globular; parallel circumferential folds poorly marked.

Adults.—Unknown.

Distribution.—Only known from type locality.

Palfuria spirembolus new species
Figs. 14, 15, 22, 29, 32, 33

Holotype.—♂, NAMIBIA: Keetmanshoop district, Khabus 146, on doleritia hill, east slope, 26°17′S, 18°14′E, 1 Oct.–8 Dec. 1988, pitfall traps, N.G. Olivier (SMNW 42286).

Paratypes.—NAMIBIA: 1♂ and a juvenile together with holotype; 1♂ from Keetmanshoop district, Dassiefontein 87, 27°13′S, 18°35′E, 7–27 Nov. 1992, pitfall traps, E. Marais (SMNW 42767); 1♀ from Kokerboom forest, 26°28′S 18°14′E, 16 Oct. 1984, under stones, E. Griffin (SMNW 43179); 1♀ from Mariental district, Berseba 170, 25°12′S, 18°03′E, 7–29 Nov. 1992, pitfall traps, E. Marais (SMNW 42880).

Table 1.—Character matrix for species of *Palfuria* and the outgroups *Heradida* and *Diores*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Diores	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heradida	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
P. caputlari	1	1	0	0	1	0	1	0	1	0	2	0	0	0	0
P. gibbosa	1	1	0	?	?	?	?	?	?	?	2	0	1	1	1
P. gladiator	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0
P. harpago	1	1	0	0	1	0	1	0	2	1	?	?	?	?	?
P. helichrysorum	1	1	0	?	?	?	?	?	?	?	2	0	0	0	1
P. hirsuta	1	1	0	?	?	?	?	?	?	?	2	1	1	0	1
P. panner	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0
P. spirembolus	1	1	0	2	0	1	2	1	3	1	1	1	1	1	2

Note: The males and the females are tentatively attributed to the same species, because both sexes were found in Keetmanshoop district.

Diagnosis.—Males of *Palfuria spirembolus* are easily identified by the long, slender embolus, the complex median apophysis and by the long carapace. Females are recognized by the accolade shape of the sclerotized rim of the epigynum, and by the internal structure of the epigynum: glandular organ present, sperm ducts long and wound, spermathecae oval. Certain of the characteristics of the secondary genital organs of this species are unique and exclude confusion with other species. *Palfuria spirembolus* appears to be closely related with *P. hirsuta* and *P. gibbosa.*

Etymology.—The species name is a contraction of *spira* (Latin for spiral) and *embolus,* referring to the long large embolus.

Male.—Total length 2.22 (2.15–2.45); carapace 1.22 long (1.03 1.47), 0.88 (0.83–0.91) wide. *Color:* Carapace medium to pale brown, with some darker, striae in thoracic area. Cephalic lobe pale brown. Eye field pale brown. Anterior part of carapace dark brown. Chelicerae medium brown, fangs dark yellow, cheliceral lamina white, sternum pale brown, with narrow darker margin; legs paler: femora pale brown, other leg segments yellow. Abdomen: dorsum shiny, dark sepia with pale circumferential folds, venter medium brown, contrast-

ing with dark sides. Branchial operculum dark brown. *Carapace:* (Fig. 32). Tegument slightly granulated: cephalic part of carapace finely granulated, cephalic lobe with stronger granulations. *Chelicerae:* Setae of cheliceral lamina curved, subequal. *Abdomen:* With scutum, modified hairs in front of spinnerets fine and long. *Eyes:* All eyes pale. a: 0.03; b: 0.07; c: 0.13; d: 0.05; e: 0.15; f: 0.11; g: 0.05; h: 0.02; MOQ: AW = 1.45 PW, AW = 1.45 L. *Clypeus:* 0.50–10× diameter of ALE. *Legs:* All leg segments covered by flattened incised hairs. Femora with two dorsal spines, three long, rigid, ventral hairs. *Male palp:* (Figs. 14, 15). Tibia with one apophysis; median apophysis pointed, funnel shaped; embolus long, slender, subtegulum present.

Female.—Total length 2.45; carapace 1.22 long (1.22–1.47), 0.84 wide (0.84–0.91). *Color:* Carapace medium brown, with some darker striae in thoracic area. Cephalic lobe brown. Eye field dark brown. Chelicerae medium brown, fangs yellow, cheliceral lamina white, sternum pale brown, with darker margin, legs paler: femora brown, other leg segments yellow. Abdomen: dorsum dark sepia with pale circumferential folds, venter pale yellow, contrasting with dark sides. Branchial operculum yellow. *Carapace:* (Fig. 33). Slightly granulated, cephalic area raised, but not slanting back. *Abdomen:* Circumferential folds not conspicuous, modified hairs in front of spin-

Table 2.—Character statistics for consensus tree with length 24, ci 0.87 and ri 0.83.

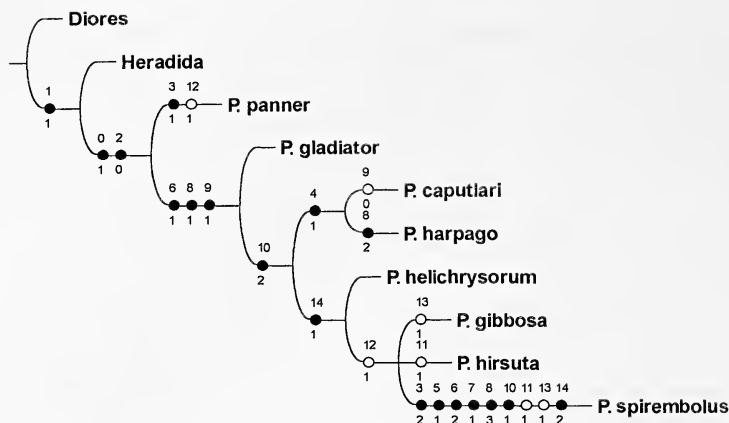| Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
steps	1	1	1	2	1	1	2	1	3	2	2	2	2	2	2
ci (× 100)	100	100	100	100	100	100	100	100	100	50	100	50	50	50	100
ri (× 100)	100	100	100	100	100	100	100	100	100	50	100	0	66	0	100

Figure 35.—Cladogram (calculated with Hennig86): strict consensus tree of two trees with length 24, consistency index 0.87 and retention index 0.83, (prepared with WINCLADA 0.99.9, Nixon 1999) under DELTRAN optimization. Numbers indicate characters (above branch) and states (under branch). Black circles: unique gains; white circles: homoplastic gains or reversals.

nerets fine and long. *Epigynum:* (Figs. 22, 29). With sclerotized, accolade-shaped line near posterior margin; internal structure complicated: with glandular organ, sperm ducts long and intricately wound. Spermathecae oval.

Distribution.—Only known from Namibia near 18°E, and between 24°–28°S.

CLADISTIC ANALYSIS

According to the cladogram presented in Jocqué (1991) *Palfuria* is part of an unresolved clade comprising several Zodariinae with femoral organ and a number of other characters (flattened leg setae, absence of leg spines, presence of patellar crack) which make this clade very robust. Among these, *Heradida* and *Palfuria* are the only genera with abdominal circumferential folds in at least some of the species. This is clear from the drawings in Jocqué (1987, fig. 4) which show the presence of these abdominal folds, a synapomorphy of *Heradida* and *Palfuria*. The fact that the genera share a large part of their distribution area further supports the assumption that *Heradida* is the sister-taxon of *Palfuria*. It is here used as one of the outgroups. The other one is *Diores* Simon 1893, which is the sister-group of the former clade plus *Acanthinozodium* Denis 1950. The following 15 characters were used to analyze the relationships among the species of *Palfuria:* 1: 'Cephalic lobe' [0] - not raised; [1] - raised; 2: 'Abdomen' [0] - without circumferential folds; [1] - with circumferential folds; 3: 'femoral organ' [0] - no deep alveolus; [1] - single mod-

ified hair in deep alveolus; 4: 'retro-lateral tibial apophysis' [0] - simple, tapered, almost straight process; [1] - srongly curved process; [2] - with broad base, broadly fused to segment; 5: 'dorsal tibial apophysis' [0] - absent; [1] - present; 6: 'embolus' [0] - short, rigid; [1] - long, flexible; 7: 'origin of embolus' [0] - far in front on tegulum; [1] - on posterior part of T, base directed retrolaterad; [2] - on prolateral part of T, base directed backwards; 8: 'Tegular swelling near base of embolus' [0] - absent; [1] - present; 9: 'median apophysis' [0] - hook-shaped; [1] - slightly curved; [2] - bifid; [3] - complex; 10: 'subtegulum' [0] - small, invisible on unexpanded palp; [1] - large, visible on unexpanded palp; 11: 'epigynum' [0] - with poorly developed transverse ridge; [1] - with sclerotized transverse ridge; [2] - with plate; 12: entrance ducts' [0] - short (< 3× diameter spermathecae); [1] - long (> 3× diameter spermathecae); 13: 'atria' [0] - absent; [1] - present; 14: 'glandular organ' [0] - absent; [1] - present; 15: 'spermathecae' [0] - spherical; [1] - narrowed towards centre; [2] - longer than wide. The character-matrix is given in Table 1.

Trees were calculated with Hennig86 (Farris 1988) and command ie* and with NONA (Goloboff 1994) with mult*15. All characters were unordered and given equal weight. In both analyses this resulted in two trees of length 24, consistency index 0.87 and retention index 0.83. The only difference between these trees is the position of *P. gibbosa* and

P. hirsuta which are either the sister-group of *P. spirembolus* alone or of *P. spirembolus* together with the other one. The strict consensus tree ("nelsen") thus only collapses this terminal clade. This cladogram, as optimized under DELTRAN, is shown in Fig. 35 (prepared with WINCLADA, Nixon 1999). A number of non-informative characters (2, 4, 6 and 8) were included mainly because the males of three species are still unknown and at least some of these characters are likely to become informative when the missing sex is found. The only effect these characters have on the analysis is a slight increase of the consistency index which drops to 0.84 when these four characters are deactivated. The retention index remains stable.

DISCUSSION

As in many other genera in the family there is a large range of complexity in male palps and female epigyna. In the male palps this ranges from the basic situation with a simple dorsolateral tibial apophysis and a short, spine-shaped embolus (*P. panner*), to a tibia with at least two apophyses as in *P. gladiator* and *P. harpago,* often combined with a long, filiform embolus as in *P. spirembolus*. In the epigynum the range is from short-to-long entrance ducts with the addition of a well separated glandular organ of which the function is unclear. It is remarkable that, here again, the basal arrangement of the secondary genitalia is more reminiscent of the primitive situation in other genera than in the most derived members of *Palfuria* itself (Jocqué 1998). Revisions of the genera *Storena* Walckenaer 1805 (Jocqué & Baehr 1992), *Diores* Simon 1893 (Jocqué 1991), *Tenedos* O.P.-Cambridge 1897 (Jocqué & Baert 1996), *Asteron* Jocqué 1991 (Baehr & Jocqué 1996) have revealed that in each of these genera the somatic characters are very stable whereas there is a wide range in the complexity of the secondary genitalia.

ACKNOWLEDGMENTS

LITERATURE CITED

Baehr, B. & R. Jocqué. 1996. A revision of *Asteron,* starring male palpal morphology (Araneae, Zodariidae). Revue Suisse de Zoologie. Vol. hors série I:15–28.

Dippenaar-Schoeman, A. & R. Jocqué. 1997. African Spiders. An Identification Manual. Plant Protection Research Institute Handbook #9. 392 pp.

Farris, J.S. 1988. Hennig86, ver. 1.5, Computer program distributed by its author.

Goloboff, P. 1994. Pee Wee and NONA, version 2.15. Computer program distributed by its author.

Jocqué, R. 1987. Descriptions of new genera and species of African Zodariidae with a revision of the genus *Heradida* (Araneae, Zodariidae). Revue de Zoologie Africaine 101:143–163.

Jocqué, R. 1990. A revision of the Afrotropical genus *Diores* (Araneae, Zodariidae). Annales du Musée Royal de l'Afrique Centrale 260:1–81.

Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201:1–160.

Jocqué, R. 1998. Female choice, secondary effect of "mate check"? A hypothesis. Belgian Journal of Zoology 128:99–117.

Jocqué, R. & B. Baehr. 1992. A revision of the Australian spider genus *Storena* (Araneae, Zodariidae). Invertebrate Taxonomy 6:953–1004.

Jocqué, R &. L. Baert. 1996. *Tenedos,* an early conquest of America. Revue Suisse de Zoologie. Vol hors série I:309–320.

Jocqué, R. & A. S. Dippenaar-Schoeman. 1992. Two new, termite-eating *Diores* species (Araneae, Zodariidae) and some observations on unique prey immobilization. Journal of Natural History 26:1405 1412.

Lessert, R. De. 1936. Araignées de l'Afrique orientale portugaise, recueillis par MM. P. Lesne et H.-B. Cot. Revue Suisse de Zoologie 43:207–306.

Lessert, R. De. 1938. Araignées du Congo Belge (Première partie). Revue de Zoologie et de Botanique Africaines 30:424–457.

Nixon, K.C. 1999. Winclada version 0.99.9. Program and documentation available from the author, Cornell University, Ithaca.

Simon, E. 1910. Arachnoidea, Araneae (II). *In* L. Schultze (ed.), Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika. Denkschriften des medicinisch-naturwissenschaftlichen Gesellschaft zu Jena 16:175–218.

CRIBELLUM AND CALAMISTRUM ONTOGENY IN THE SPIDER FAMILY ULOBORIDAE: LINKING FUNCTIONALLY RELATED BUT SEPARATE SILK SPINNING FEATURES

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ABSTRACT. The fourth metatarsus of cribellate spiders bears a setal comb, the calamistrum, that sweeps over the cribellum, drawing fibrils from its spigots and helping to combine these with the capture thread's supporting fibers. In four uloborid species (*Hyptiotes cavatus*, *Miagrammopes animotus*, *Octonoba sinensis*, *Uloborus glomosus*), calamistrum length and cribellum width have similar developmental trajectories, despite being borne on different regions of the body. In contrast, developmental rates of metatarsus IV and its calamistrum differ within species and vary independently among species. Thus, the growth rates of metatarsus IV and the calamistrum are not coupled, freeing calamistrum length to track cribellum width and metatarsus IV length to respond to changes in such features as combing behavior and abdomen dimensions.

Keywords: Cribellar thread, *Hyptiotes cavatus*, *Miagrammopes animotus*, *Octonoba sinensis*, *Uloborus glomosus*

Members of the family Uloboridae produce cribellar prey capture threads formed of a sheath of fine, looped fibrils that surround paracribellar and axial supporting fibers (Eberhard & Pereira 1993; Opell 1990, 1994, 1995, 1996, 1999; Peters 1983, 1984, 1986). Cribellar fibrils come from the spigots of an oval spinning field termed the cribellum (Fig. 1; Kovoor & Peters 1988; Opell 1994, 1999), located on the ventral surface of the spider's abdomen, just anterior to its spinnerets. These fibrils are drawn from cribellar spigots by the calamistrum, a setal comb that is formed of a single row of long, slender, curved setae that extends along the proximal ½–⅔ of both fourth metatarsi (Fig. 2; Kullmann & Stern 1981; Opell 1979; Peters 1983, 1984). When drawing fibrils from the cribellum, uloborids brace the tarsus of the combing leg on the metatarsus of the opposite fourth leg (Eberhard 1988; Opell 1979; Peters 1984). Left and right legs are used alternately in short, vigorous bouts of combing (Eberhard 1988) and the resulting sheet of fibrils is compressed around supporting fibers by adductions of the posterior lateral spinnerets (Peters 1984).

In members of the family Uloboridae, spiderlings hatch from eggs, molt once within the egg sac, and emerge from the egg sac as second instars (Opell 1979). However, their cribella and calamistra are not functional until they molt again to become third instars. Second instar orb-weaving uloborid species produce a juvenile web that lacks a sticky spiral and has many closely spaced radii (Lubin 1986). Members of the triangle-web genus *Hyptiotes* Walckenaer 1837 and the simple-web genus *Miagrammopes* O. Pickard-Cambridge 1869 do not construct capture webs until they become third instars. After emerging from the egg sac, second instar *Hyptiotes* rest on vegetation (Opell 1982a, b), whereas *Miagrammopes* cling to the outer surface of their cylindrical egg sac, which is still held by the female (Lubin, et al. 1978; Opell 2001). When spiders mature as sixth instars (Berland 1914; Opell 1982a, 1987), females retain a functional cribellum and calamistrum, but males do not (Opell 1989, 1995).

Complementary structures like the cribellum and calamistrum must develop in consort if they are to function throughout a spider's life. As the cribellum is borne on the abdomen and the calamistrum on the fourth legs, this requires a convergence in the developmental rates of structures on different body regions. If the growth rates of the calamistrum and metatarsus IV are linked, then both must de-
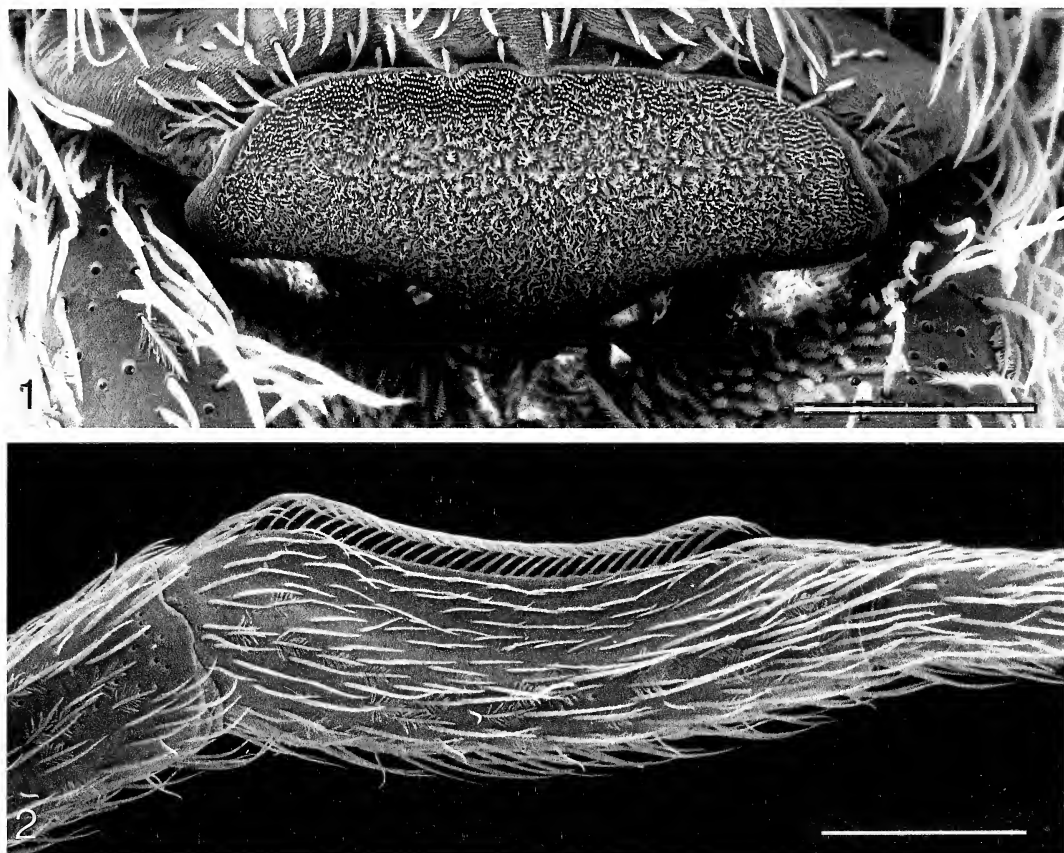
Figures 1, 2.—The cribellum (Fig. 1, scale bar = 150 μm), and calamistrum (Fig. 2, scale bar = 250 μm) of an adult female *Miagrammopes animotus*.

velop at a rate that equals or exceeds that of cribellum width. If these structures develop at different rates, then only calamistrum length must increase at a rate that equals or exceeds that of cribellum width. I hypothesize that the latter occurs, as this would not compromise other fourth leg functions or require compensatory changes in the lengths of other fourth leg articles.

I tested this hypothesis by comparing the developmental rates of structures within the orb-weaving species *Uloborus glomosus* (Walckenaer 1841) and *Octonoba sinensis* (Simon 1880) and the reduced-web species *Hyptiotes cavatus* (Hentz 1847) and *Miagrammopes animotus* Chickering 1968. The orb is the plesiomorphic web form in the Uloboridae and the triangle-web and simple-web are derived forms (Coddington 1990; Opell 1979).

METHODS

I collected 102 *U. glomosus* (39 of which were adult) from shrubbery on the Virginia Tech campus in Montgomery County, Virginia during the spring and summer of 1989. *Octonoba sinensis* is an introduced Asian species. I collected 79 individuals (17 of which were adults) in greenhouses on the Virginia Tech campus during the spring and summer of 1989. I collected 136 *H. cavatus* (31 of which were adult) from Giles and Montgomery Counties, Virginia during the spring and summer of 1990. I collected 190 *M. animotus* (77 of which were female) from the Center for Energy and Environment Research's El Verde Research Station, Luquillo National Forest, Puerto Rico during the summer of 1990. Only one species of each genus was present at each locality, so there were no problems in determining the species of juvenile specimens. All instars of *M. animotus* were present at the same time. Successive instars of the other species were collected as they appeared during the spring and summer. These species were identified using the revisions of Chickering
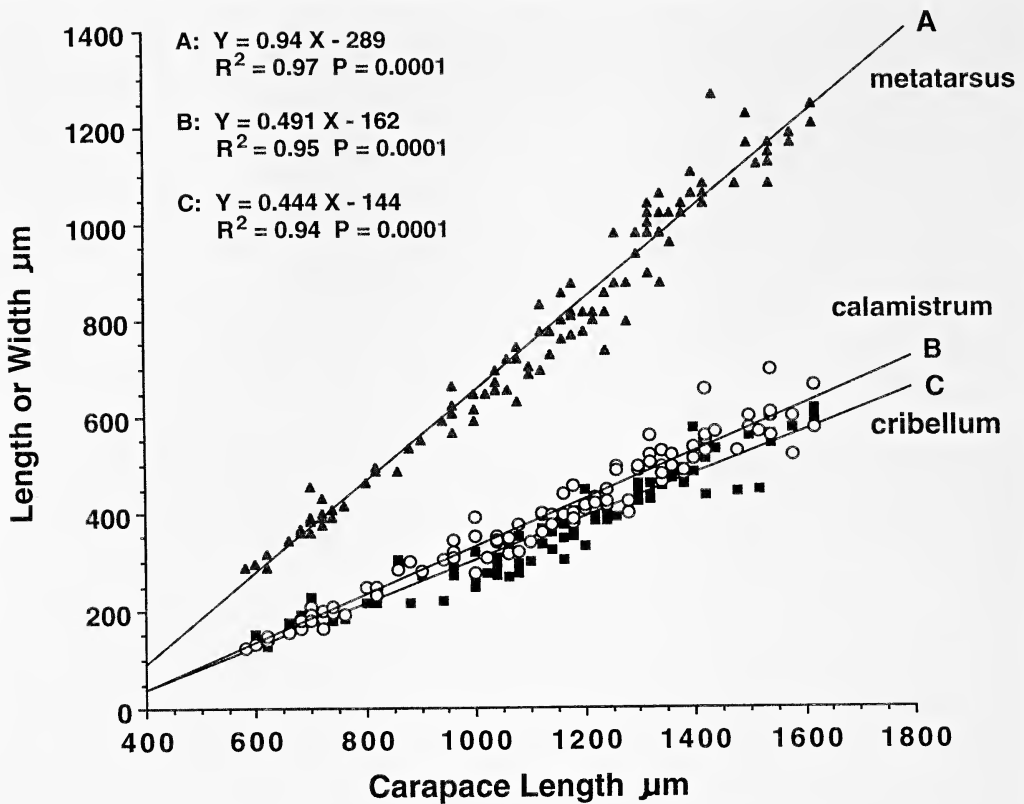
A: $Y = 0.94\,X - 289$
$R^2 = 0.97$ $P = 0.0001$

B: $Y = 0.491\,X - 162$
$R^2 = 0.95$ $P = 0.0001$

C: $Y = 0.444\,X - 144$
$R^2 = 0.94$ $P = 0.0001$

Figure 3.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Uloborus glomosus*. Sample size = 102.

(1968), Muma & Gertsch (1964), and Opell (1979). Voucher specimens are deposited in the Museum of Comparative Zoology.

Specimens were preserved in 80% ethanol. I measured the carapace length of each spider under a dissecting microscope. Each specimen's cribellum and fourth leg were then removed and mounted in water soluble medium under a cover slip on a microscope slide. Using a compound microscope, I measured cribellum width, fourth metatarsus length, and calamistrum length. All features were measured to at least the nearest 20 μm. I measured calamistrum length as the distance separating the proximal- and distal-most setal bases. This approach eliminates problems associated with missing setae and it does not make any assumptions about the deflection of calamistrum setae during cribellar fibril combing. Statistical tests were performed with SAS (SAS Institute Inc., Cary, North Carolina). P values of ≤0.05 were considered significant.

RESULTS

Figures 3–6 plot cribellum, calamistrum, and metatarsus IV lengths against carapace length in the four species studied. Each of these regressions is significant ($F = 584$–2951, $P = 0.0001$). As reflected by R^2 values, the variance of these features is greater in *H. cavatus* and *M. animotus* than it is in *U. glomosus* and *O. sinensis*. This may be the result of measurement precision, as *H. cavatus* and *M. animotus* are smaller than *U. glomosus* and *O. sinensis*. However, the smaller values of the axes of *H. cavatus* and *M. animotus* (Figs. 5, 6) tend to exaggerate the scatter of these species' points. Homogeneity tests show that, for each species, the slope of calamistrum length exceeds that of cribellum width ($F = 8.77$–80.58, $P = 0.0034$–0.0001) and the slope of metatarsus IV length exceeds that of calamistrum length ($F = 17.45$–482.30, $P = 0.0001$). In *M. animotus* the intercepts of cribellum width and calamistrum length differ (t
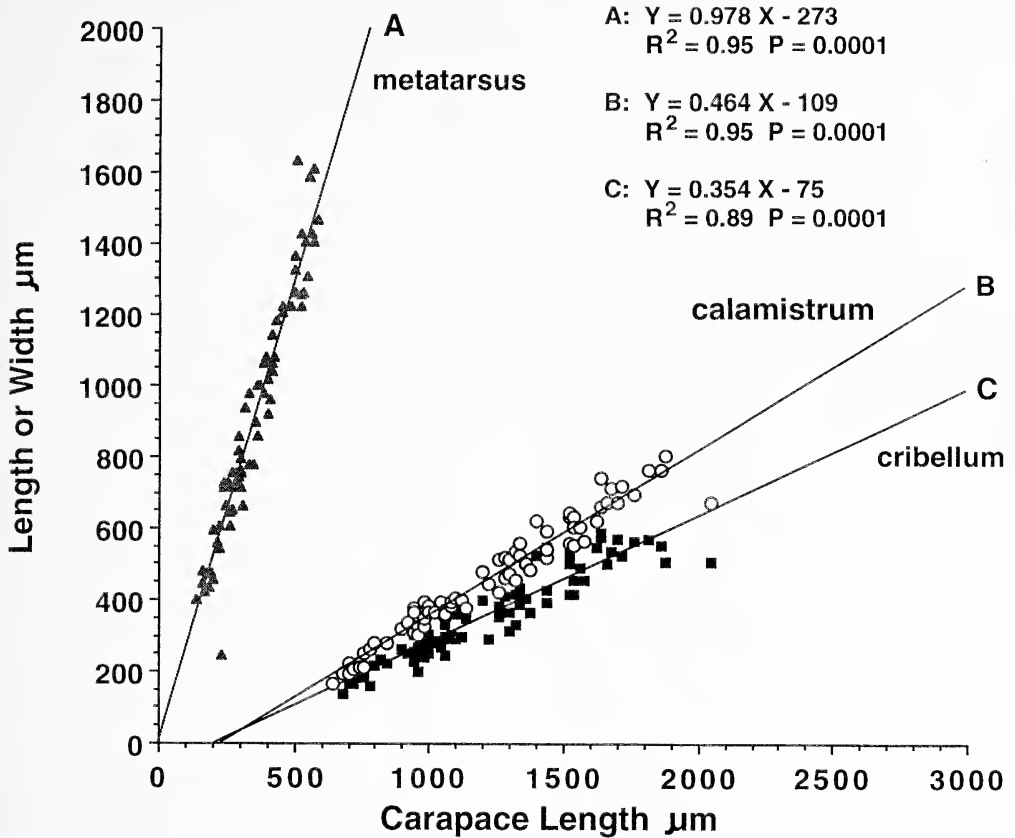
Figure 4.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Octonoba sinensis*. Sample size = 79.

= 2.558, P = 0.015), but in the other three species they do not (t = 0.993–1.698, P = 0.100–0.285). Thus, in each species, calamistrum length and cribellum width are initially very similar, but calamistrum length increases more rapidly than cribellum width.

Tests of the homogeneity of the regression slopes of metatarsus IV show the slopes of *U. glomosus* and *O. sinensis* do not differ (F = 1.63, P = 0.204). The slope of *U. glomosus* (the smaller of the two orb-web species' values) is greater than that of both *H. cavatus* (F = 70.73, P = 0.0001) and *M. animotus* (F = 330.98, P = 0.0001). Developmental rates of the calamistrum also differ but do not mirror differences in metatarsus IV development. If they did, calamistrum length would increase at a rate less than that of the cribellum in *H. cavatus* and *M. animotus*. However, as documented above, in all species calamistrum length increases more rapidly than does cribellum width.

The slopes of the calamistrum of *U. glo-*

mosus and *O. sinensis* do not differ (F = 2.60, P = 0.109). The slope of *U. glomosus* (the smaller of these values) is less than that of *H. cavatus* (F = 11.94, P = 0.0007) and greater than that of *M. animotus* (F = 11.69, P = 0.0007). The metatarsus IV of *H. cavatus* has a slope that is 0.229 less than that of *U. glomosus*, but its calamistrum has a slope that is 0.066 greater. In *M. animotus*, these values are −0.446 and −0.071, respectively. This is further documentation that the slopes of metatarsus IV and its calamistrum are free to assume different trajectories.

DISCUSSION

The results of this study support the hypothesis that developmental rates of metatarsus IV and the calamistrum differ. By developing at a slower rate than the leg article that bears it, calamistrum length tracks more closely the development of the cribellum, with
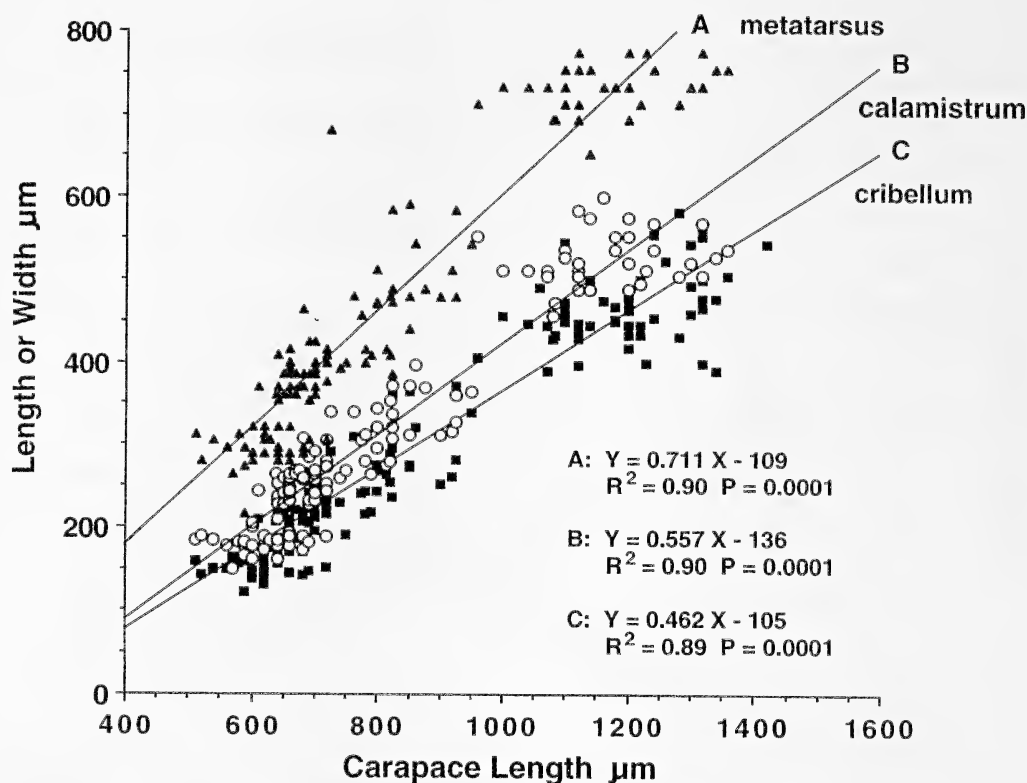
Figure 5.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Hyptoites cavatus*. Sample size = 136.

which it is functionally linked. I did not examine possible correlates of metatarsus IV length. However, changes in the lengths of the fourth leg articles may be associated with changes in abdomen length and may serve to maintain the proper alignment of the calamistrum as it passes over the cribellum. Calamistrum length and cribellum width are initially very similar, but calamistrum length increases at a slightly greater rate. If a calamistrum is to comb all the fibrils from cribellum spigots as it passes over the cribellum and is held with its length parallel to the transverse axis of the cribellum, then calamistrum length must equal cribellum width. As the angle formed by the calamistrum and the transverse axis of the cribellum increases, calamistrum length must increase if it is to completely span the cribellum. For example, at an angle of 15°, the calamistrum must be 4% longer, and at an angle of 30°, 16% longer than if it were held at an angle of 0°. If the calamistrum moves laterally as it sweeps across the cribellum, further increases in calamistrum length

would be necessary to ensure that the calamistrum completely spans the cribellum. Thus, the developmental increase of calamistrum length relative to cribellum width observed in this study may reflect increases in the angle at which the calamistrum passes over the cribellum or the lateral movement of its passage. These changes may be necessary to accommodate changes in the lengths of fourth leg articles or changes in abdomen length or width that require the fourth legs to assume different postures during the production of cribellar thread.

Within the family Uloboridae, web reduction is associated with a reduction in the length of metatarsus IV relative to the carapace length. In *U. glomosus* and *O. sinensis* adult females this ratio is 0.75 and 0.83, respectively. In *H. cavatus* and *M. animotus* this ratio is 0.63 and 0.56, respectively (Opell, unpubl. obs.). In contrast, the cribella of these two reduced-web species have greater numbers of spinning spigots than do the orb-weaving species (Opell 1994). Thus, unless meta-
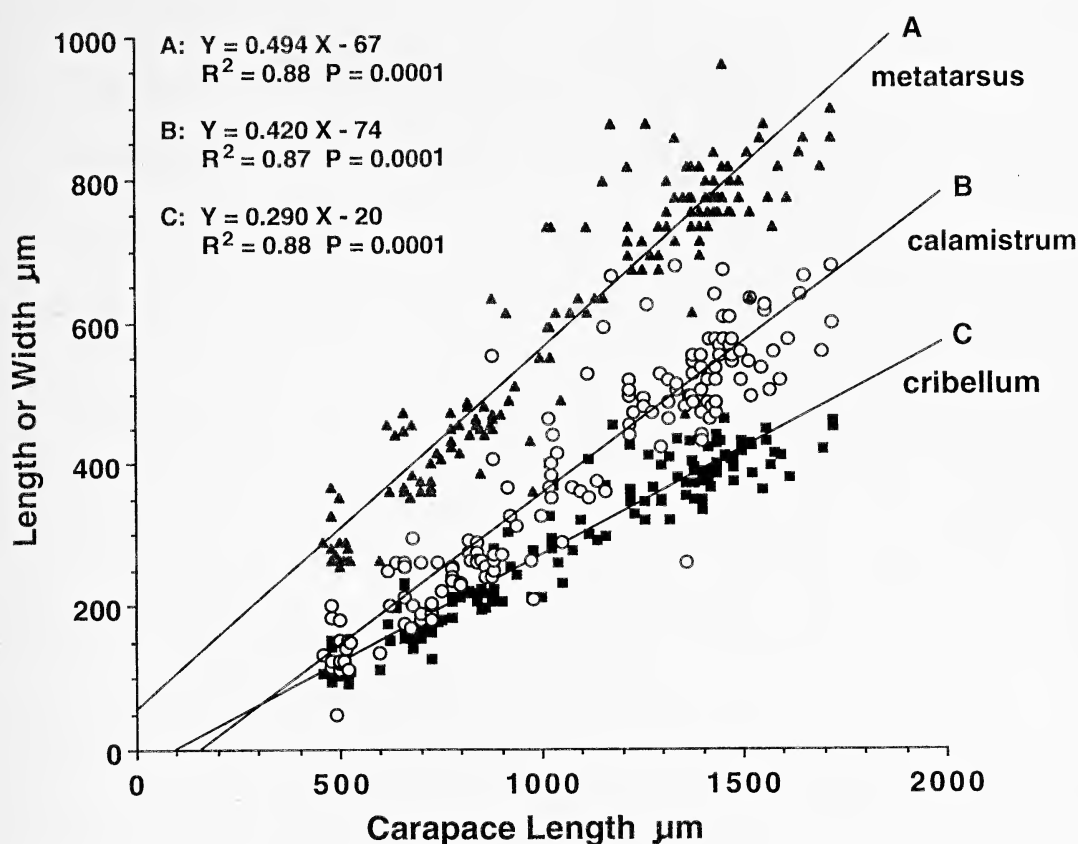
Figure 6.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Miagrammopes animotus*. Sample size = 190.

tarsus IV and the calamistrum have different developmental trajectories, increases in calamistrum length could not keep pace with the increases in cribellum width that are necessary to accommodate a greater number of spigots and produce wider, stickier cribellar threads (Opell 1995).

The strong ontogenetic linkage of cribellum width and calamistrum length observed in this study contrasts with the weak phylogenetic relationship between these features observed by Opell et al. (2000). In that study no correlation between cribellum width and calamistrum length could be demonstrated among representatives of different families or among genera of the family Uloboridae. Only among species of the dictynid genus *Mallos* O. Pickard-Cambridge 1902 was there an association between these features, and this regression had an R^2 value of 0.41 compared to a mean value of 0.93 for the developmental studies reported here. As Opell et al. (2000) point out,

differences in abdomen dimensions and cribellar thread combing behaviors among species probably explain the weak relationship between cribellum width and calamistrum length at more inclusive taxonomic levels.

ACKNOWLEDGMENTS

LITERATURE CITED

Berland, J. 1914. Note sur le cycle vital d'une Araignée cribellate, *Uloborus plumipes* Lucus. Archives de Zoologie Expérimentale et Générale. Notes et Revue 54:45–57.

Chickering, A.M. 1968. The genus *Miagrammopes* (Araneae, Uloboridae) in Panama and the West Indies. Breviora (Museum of Comparative Zoology) 289:1–28.

Coddington, J.A. 1990. Ontogeny and homology in the male palpus of orb-weaving spiders and

their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496:1–52.

Eberhard, W.G. 1988. Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic implications. Bulletin of the British Arachnological Society 7:247–251.

Eberhard, W.G. & F. Pereira. 1993. Ultrastructure of cribellate silk of nine species in eight families and possible taxonomic implications. (Araneae: Amaurobiidae, Deinopidae, Desidae, Dictynidae, Filistatidae, Hypochilidae, Stiphidiidae, Tengellidae). Journal of Arachnology 21:161–174.

Kovoor, J. & H.M. Peters. 1988. The spinning apparatus of *Polenecia producta* (Araneae, Uloboridae): Structure and histochemistry. Zoomorphology 108:47–59.

Kullmann, E & H. Stern. 1975. Leben am seidenen Faden. Bertelsmann Verlag, München.

Lubin, Y.D. 1986. Web building and prey capture in the Uloboridae. Pp. 132–171. *In* Spiders: Webs, Behavior, and Evolution (W.A. Shear, ed.),. Stanford Univ. Press, Stanford.

Lubin, Y.D., W.G. Eberhard, & G.G. Montgomery. 1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche 85:1–23.

Muma, M.M. & W.J. Gertsch. 1964. The spider family Uloboridae in North America north of Mexico. American Museum Novitates 2196:1–43.

Opell, B.D. 1979. Revision of the genera and tropical American species of the spider Family Uloboridae. Bulletin of the Museum of Comparative Zoology 148:433–549.

Opell, B.D. 1982a. Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). Journal of Arachnology 10:185–191.

Opell, B.D. 1982b. Cribellum, calamistrum, and ventral comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). Bulletin of the British Arachnological Society 5:338–343.

Opell, B.D. 1987. Changes in web-monitoring forces association with web reduction in the spider family Uloboridae. Canadian Journal of Zoology 65:1028–1034.

Opell, B.D. 1989. Functional associations between the cribellum spinning plate and prey capture threads of *Miagrammopes animotus* (Araneida, Uloboridae). Zoomorphology 108:263–267.

Opell, B.D. 1990. The material investment and prey capture potential of reduced spider webs. Behavioral Ecology and Sociobiology 26:375–381.

Opell, B.D. 1994. Factors governing the stickiness of cribellar prey capture threads in the spider family Uloboridae. Journal of Morphology 221:111–119.

Opell, B.D. 1995. Ontogenetic changes in cribellum spigot number and cribellar prey capture thread stickiness in the spider family Uloboridae. Journal of Morphology 224:47–56.

Opell, B.D. 1996. Functional similarities of spider webs with diverse architectures. American Naturalist 148:630–648.

Opell, B.D. 1999. Changes in spinning anatomy and thread stickiness associated with the origin of orb-weaving spiders. Biological Journal of the Linnean Society 68:593–612.

Opell, B.D., J.S. Sandidge & J.E. Bond. 2000. Exploring Functional Associations Between Spider Cribella and Calamistra. Journal of Arachnology 28:43–48.

Opell, B.D. 2001. Egg sac recognition by female *Miagrammopes animotus* (Araneae, Uloboridae). Journal of Arachnology 29:244–248.

Peters, H.M. 1983. Struktur und Herstellung der Fangfäden cribellater Spinnen (Arachnida: Araneae). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 26:241–253.

Peters, H.M. 1984. The spinning apparatus of Uloboridae in relation to the structure and construction of capture threads (Arachnida, Araneida). Zoomorphology 104:96–104.

Peters, H.M. 1986. Fine structure and function of capture threads. In Ecophysiology of Spiders (W. Nentwig, ed.), Pp. 187–202. Springer Verlag, New York.

DOES THE STRUCTURAL COMPLEXITY OF AQUATIC MACROPHYTES EXPLAIN THE DIVERSITY OF ASSOCIATED SPIDER ASSEMBLAGES?

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ABSTRACT. Differences in species richness and species composition of spiders associated with aquatic macrophytes of different structural complexities were examined in the Pantanal floodplain of Mato Grosso do Sul, Brazil. The plants studied were *Nymphaea amazonum* (Nymphaeaceae), *Salvinia auriculata* (Salviniaceae), *Echinodorus paniculatus* (Alismataceae) and *Eichhornia azurea* (Pontederiaceae), whose classes of complexity were determined based on their leaf and branch densities, vertical structure, and height. Data were collected from 62 monospecific plant patches in temporary lentic environments. A total of 235 spiders of 33 species in 13 families was collected. *Nymphaea amazonum,* the plant with the lowest complexity class, did not provide adequate sites for the establishment of spiders, and only four individuals of four spider species were found on its patches. *Salvinia auriculata* and *E. paniculatus* shared the intermediate class of complexity, but showed statistically significant differences in composition and richness of spider species. In *E. paniculatus,* greater height and lower leaf and branch densities favored the establishment of web weavers, whereas the smaller height and higher density of *S. auriculata* promoted the occurrence of wandering spiders. *Eichhornia azurea,* the plant with the highest complexity class, presented the greatest number of unique spider species, differing from the other plants in spider species composition. Results indicate that richness and composition of spider species associated with aquatic macrophytes in the study site are influenced by the structural complexity of these plants.

Keywords: Araneae, community structure, South Pantanal, species composition, species richness

Habitat structural complexity can affect species diversity (Pianka 1978; Robinson 1981; Gunnarson 1988; Cornell & Lawton 1992; Shorrocks & Sevenster 1995; Balfour & Rypstra 1998). This hypothesis has been supported by studies focusing on different animal species in several environments (Pianka 1966, 1967; Murdock et al. 1972; Uetz 1975, 1977; Hatley & MacMahon 1980; Dueser & Porter 1986; Dean & Connell 1987; Pearsons et al. 1992). It has been shown, for example, that the vertical structure of vegetation in North American temperate forests is a better indicator of bird diversity than the diversity of plant species with which the birds are associated (MacArthur & MacArthur 1961).

Spatial and architectural features of habitat structure can determine diversity, density, and distribution of spider species (Hatley & MacMahon 1980; Balfour & Rypstra 1998). Similarly, environmental physiognomy (for instance, open or closed forest; dense or sparse litter layer) and physical structure can significantly influence spider habitat preference (Jennings et al. 1988; Uetz 1991). Number and dominance of spider species tend therefore to be highly related to the structure of the plant community on which they occur (Gunnarsson 1990; Uetz 1991; Baur et al. 1996). These relationships among plant and spider communities appear to be determined primarily by the structural complexity of the plant, which can provide, for example, a variety of retreats and attachment sites for webs, as well as favorable microclimatic conditions (Hatley & MacMahon 1980; Pulz 1987).

Few are the studies performed on the association of spiders and aquatic macrophytes, and on the effects of the structural complexity of aquatic macrophytes on the community structure of associated spider species. Even these studies, however, have been limited to reporting the occurrence of spiders on those plants (e.g., Merck 1988; Heckman 1994) or to describing new species (Brescovit et al. 2000).

The present work examined the influence of plant structural complexity on spider com-

munities associated with aquatic macrophytes in the southern Pantanal, Brazil, by evaluating the variation of spider species composition and richness on four plant species.

METHODS

Study site.—The Pantanal is a floodplain of *ca.* 140,000 km^2 located in central South America, mainly within Brazil. This area is, in fact, an assemblage of diverse landscapes occupying the hydrographic sub-basins of the Paraguay watershed. Each of these sub-basins has its characteristic hydrologic regimes, soil types, and geologies, which affect fauna and flora distribution (Boggiani & Coimbra 1996).

The present study was carried out in a Pantanal sub-region known as "Pantanal do Miranda e Abobral" (*sensu* Adámoli 1982), located in Mato Grosso do Sul state, southwestern Brazil (19°22′–19°33′S; 57°2′–57°3′W). The climate is characterized by a wet season extending from December–May and a dry one from June–November. All samples were collected from temporary lentic environments located in the vicinity of a 25 km stretch of the MS-184 road. These lentic environments are formed by depressions in the terrain that remain inundated by nearby rivers or filled with rainwater for most of the wet season, resulting in temporary ponds. When rains end and rivers start to recede, the water level in these ponds begins to fall, and they eventually disappear during the dry season. Because of this cycle, data collection had to be limited to the period when water was not entirely depleted.

Aquatic macrophytes.—The plants investigated were *Nymphaea amazonum* Mart. & Zucc. (Nymphaeaceae), *Salvinia auriculata* Aublet (Salviniaceae), *Echinodorus paniculatus* Mich. (Alismataceae), and *Eichhornia azurea* (Sw.) Kunth (Pontederiaceae), which are illustrated in Fig. 1. The floating leaves of *N. amazonum* have glabrous, membranous, orbicular, laminate limbs and lie flat on the water surface, forming a discontinuous, thin, flat carpet. Patches of *S. auriculata* resemble a continuous, thick, curly carpet formed by upright chains of smaller, floating leaves. This is a herbaceous plant with short petioles and pilose, oval limbs. *Echinodorus paniculatus,* another herbaceous plant, has long triangular petioles and leaves that emerge vertically or obliquely. Limbs are glabrous, coriaceous and

lanceolate. *Eichhornia azurea,* also herbaceous, has leaves that emerge vertically or obliquely; but its petioles are cylindrical, shorter than those of *E. paniculatus* and have a sheath. Limbs are glabrous, fleshy and obovate.

Quantification of the structural complexity of aquatic macrophytes.—The structural complexity of monospecific patches of those four aquatic macrophytes was quantified by measuring plant density, height and vertical structure above the water surface, based on the methodology of Balfour & Rypstra (1998). Ten patches of each plant were sampled, employing a 1 m^2 floating PVC frame whose sides were numbered at 10 cm intervals, thus defining an orthogonal grid. Numbering ran from 0–10 on one of the sides, then proceeded from 11–21 on the adjacent side (with numbers 10 and 11 coinciding on the corner edge). On the remaining two sides, these integer sequences (0–10, 11–20) were repeated so as to mirror those parallel to them.

In order to measure plant density in each sample, an integer from 0–21 was drawn. A horizontal line was then positioned connecting the same two integers lying on opposite sides of the frame, and the number of branches and leaves touching this line was recorded.

For measuring the vertical structure of the plants, two integers were drawn, one of them from 0–10 and the other from 11–21. Two horizontal lines were thus determined, at whose intersection a third, vertical line was positioned. The number of leaves and branches touching this vertical line was recorded. Plant height was considered as the highest point at which the plant touched this vertical line.

To determine the structural complexity classes of the plant patches, the differences among the variables considered were tested by analysis of variance (ANOVA) and Tukey test ($\alpha = 0.05$). Three possible arbitrary values were then assigned to the means of those variables: value 0 to the smallest mean, 1 to the intermediate, and 2 to the greatest mean.

Data sampling.—Data were collected from 13 ponds from November 1994 to April 1997. A total of 62 monospecific patches was sampled, namely, 12 of *N. amazonum,* 18 of *S. auriculata,* 10 of *E. paniculatus,* and 22 of *E. azurea.* Patch area was estimated and subdivided in numbered sub-areas of 1 m^2, and one
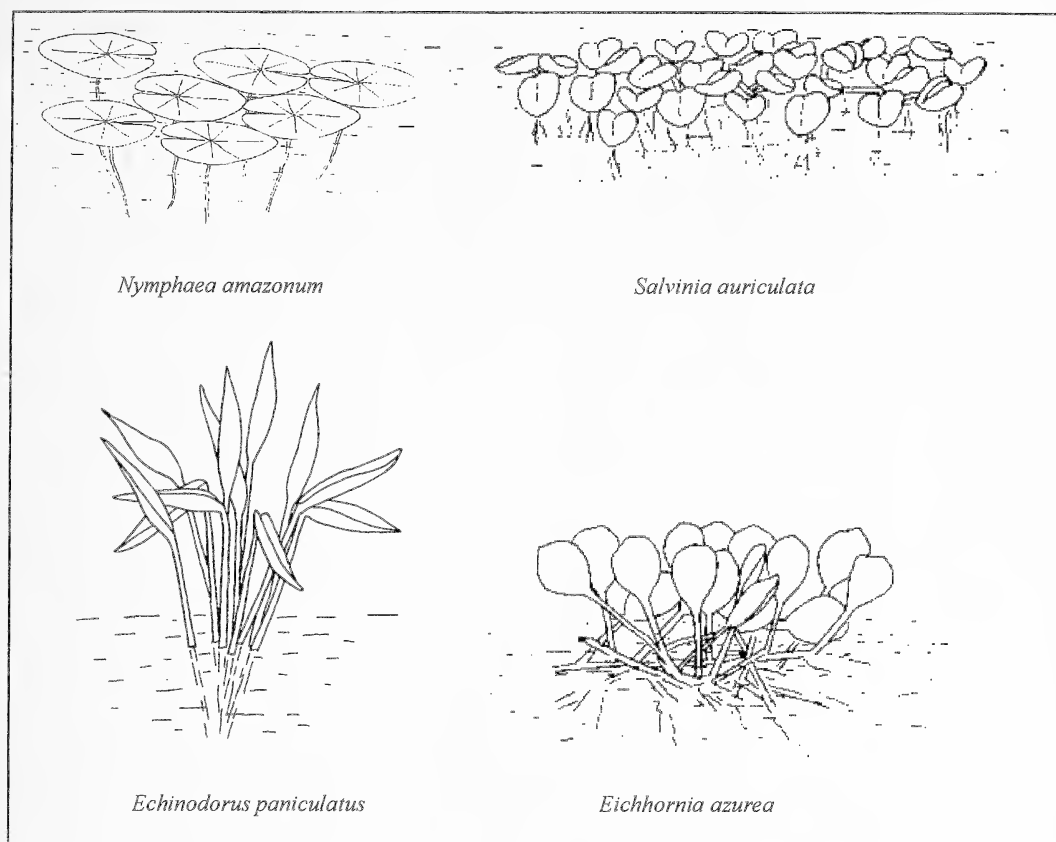
Figure 1.—Schematic depiction of the four aquatic macrophyte species investigated. *Nymphaea amazonum* forms a thin mat that lies flat on the water surface. *Salvinia auriculata* forms a mat that is rich in recesses and projections. *Echinodorus paniculatus* has stems that emerge vertically or obliquely without ever forming a mat. The carpet formed by *Eichhornia azurea* is also rich in recesses and projections, but has a series of vertical and oblique emerging stems.

of them was randomly chosen as the sampling point for that patch. This sampling area was delimited with the help of a 1 m² floating PVC frame whose sides were fitted with a 15 cm high nylon-mesh screen to prevent spiders from escaping. At all sampling points, plant species richness had value 1. All spiders visually located were collected for identification, and their voucher specimens are deposited in the Museum of Instituto Butantan, São Paulo.

Spider species composition and richness.—In order to compare spider species richness among the plant species, the smallest sample size (number of individuals collected associated with one of the plant species) was considered, since species richness is dependent on the number of individuals sampled. Spider species richness was then estimated for each plant species by rarefaction, using the software RAREFACT (Krebs 1989). The expected number of species and the standard deviation for each complexity class were thus obtained. Species richness was considered to differ among complexity classes if no overlap occurred between the intervals generated by the standard deviation of species richness for each sample. The mean numbers of spider species per sample were statistically compared among the plant species by analysis of variance. The mean number of spider species and the number of individuals, both grouped by guild (web or wandering spiders), were also analyzed (ANOVA, Tukey test, and χ^2 test of independence, $\alpha = 0.05$).

RESULTS

Quantification of plant structural complexity.—Results obtained for the structural

complexity of the monospecific patches of aquatic macrophytes are shown in Table 1. Complexity class was lowest for *N. amazonum* (class 0) and highest for *E. azurea* (class 4). No plant species fitted classes 1 or 2. *Salvinia auriculata* and *E. paniculatus* shared the same complexity class (class 3), despite differences found in the variables involved in its determination: *S. auriculata* presented greater density and smaller height, whereas for *E. paniculatus* density was smaller and height was greater. *Eichhornia azurea* provided the greatest value for vertical structure, but its values for plant density and height were intermediate. *Nymphaea amazonum* did not show any variation in either height or vertical structure (both at value 0), and its density never exceeded three leaves per meter.

Spider species composition and richness.—A total of 235 spiders belonging to 33 species was found (Table 2). Because some of the individuals collected were juvenile, they could only be taxonomically identified down to family or genus level. Only four individuals—and each of these of a different species—were found on *N. amazonum.* Their occurrence was regarded as fortuitous, and the corresponding data were excluded from the composition and richness analyses. As for the other three plants, 15 spider species (63 individuals) were found on *S. auriculata,* 14 species (54 individuals) on *E. paniculatus,* and 24 species (114 individuals) on *E. azurea.* Four species of spiders were common to these three plant species. Regarding composition, *E. azurea* presented the greatest number of unique spider species (9 species; 37.5%), followed by *S. auriculata* (5 species; 33.33%) and *E. paniculatus* (3 species; 21.43%). The smallest overlap in species composition occurred between *S. auriculata* and *E. paniculatus,* with only 5 common species (*ca.* 35%). Four of these five species were also common to *E. azurea,* accounting for 39.15% of the overall total of individuals collected.

Overall, wandering spiders outnumbered web weavers, both in the number of species and of individuals (Table 2). Wandering individuals accounted for 66.23% of the total collected (Fig. 2). When only those animals collected from *E. paniculatus* are considered, the proportion of wandering individuals falls to ca. 37% (Fig. 2). The proportions between wandering and web spiders differed signifi-

cantly among the three plants analyzed (χ^2 = 8.05, df = 2, P < 0.02, Fig. 2). The proportion of individuals between guilds was higher for wandering spiders on both *S. auriculata* and *E. azurea,* but higher for web spiders on *E. paniculatus.*

As to richness, the expected number of spider species arrived at by employing the rarefaction method differed among plant species. By applying this method to the 54 individuals found on *E. paniculatus* (the smallest number of spiders found on any of the three plants analyzed), the number of spider species could be estimated at 18.89 (SD ± 1.56) for *E. azurea,* 14.10 (SD ± 0.84) for *S. auriculata,* and 14 for *E. paniculatus* (Table 2). Taking into account the intervals generated by the standard deviation of the expected number of species, *E. azurea* presented the greatest richness, whereas *S. auriculata* and *E. paniculatus* did not differ from each other. Statistical analysis of the data on spider species number per sample for each plant species did not reveal any significant differences among the three plants analyzed (ANOVA, F = 0.598, df = 2, P = 0.545). However, when the numbers of spider species per guild were compared among the plants, *E. paniculatus* showed the greatest richness of web spiders and the smallest one of wandering spiders, whereas *S. auriculata* and *E. azurea* did not differ significantly from each other (Table 3).

DISCUSSION

Nymphaea amazonum, the plant with the lowest structural complexity, had the lowest richness of spiders, with four species but only one individual of each (Table 2). The occurrence of these was regarded as fortuitous, since the same four species were abundantly found on all the other macrophytes (Raizer 1997). This is indicative that *N. amazonum* does not favor the establishment of a community of associated spiders. In fact, because its leaves are smooth and lie flat on the water surface, this plant does not provide microsites for oviposition, molting, or construction of any kind of web or retreat. Spiders living on these leaves would also be directly exposed to solar radiation, which favors dehydration (Pulz 1987). Furthermore, potential prey (such as diptera and orthoptera) are rarely found on *N. amazonum* (Raizer pers. obs.).

Spider species composition varied not only

Table 1.—Structural complexity of monospecific patches of aquatic macrophytes in southern Pantanal, calculated from the following variables: plant density (leaves and branches per meter), vertical structure of the plant (number of branches and leaves), and plant height (in centimeters). Values for the same variable that are followed by the same letter do not differ statistically (Tukey test, $\alpha = 0.05$). For each variable, complexity was assigned values 0, 1, or 2, depending on statistical differences or similarities ($a = 0$; $b = 1$; $c = 2$). For each plant species, the structural complexity class is the sum of the complexities of each variable.

	Nymphaea amazonum	Salvinia auriculata	Echinodorus paniculatus	Eichhornia azurea	ANOVA results
Plant density (mean ± SD)	2.60 ± 0.52a	95.10 ± 17.38c	6.30 ± 5.17a	35.40 ± 4.55b	$F = 209.252$, df = 3, $P < 0.001$
Plant vertical structure (mean ± SD)	0.00 ± 0.00a	2.80 ± 1.23b	3.30 ± 1.70b	6.90 ± 2.13c	$F = 35.866$, df = 3, $P < 0.001$
Plant height (mean ± SD)	0.00 ± 0.00a	1.81 ± 1.15a	80.30 ± 29.02c	54.95 ± 11.55b	$F = 65.175$, df = 3, $P < 0.001$
Value of plant density complexity	0	2	0	1	—
Value of plant vertical structure complexity	0	1	1	2	—
Value of plant height complexity	0	0	2	1	—
Plant structural complexity class (sum of the 3 previous values)	0	3	3	4	—

Table 2.—Abundance of spider species collected from monospecific patches of four species of aquatic macrophytes in southern Pantanal. (Plants: NA = Nymphaea amazonum, SA = Salvinia auriculata, EP = Echinodorus paniculatus, EA = Eichhornia azurea. Spider guilds: WAN = wandering spiders, WEB = web spiders.) Number of samples, mean number of spider species, and richness obtained by rarefaction are also indicated.

Spiders	Number of individuals sampled per plant species				Guilds	
	NA	SA	EP	EA	WAN	WEB
Anyphaenidae						
Osoriela rhodonota Mello-Leitão	0	0	0	2	X	
Otoniela sp.	0	0	1	4	X	
Araneidae						
Actinosoma pentacanthum (Walckenaer)	0	10	0	1		X
Alpaida veniliae (Keyserling)	0	0	7	1		X
Araneus guttatus (Keyserling)	0	1	0	1		X
Eustala sp.	0	0	0	1		X
Metazygia gregalis (O. P.-Cambridge)	0	2	16	5		X
sp1 (not identified)	0	0	0	6		X
Ctenidae						
Neoctenus comosus Simon	0	0	0	2	X	
Dictinidae						
sp1 (not identified)	0	0	0	1	X	
Linyphiidae						
sp1 (not identified)	0	0	0	2		X
Lycosidae						
Hogna sp	1	18	2	13	X	
Lycosa nyethemera Bertkau	0	5	0	12	X	
sp1 (not identified)	0	4	1	7	X	
sp2 (not identified)	0	7	0	0	X	
sp3 (not identified)	0	0	0	1	X	
Pisauridae						
Ancylometes concolor (Perty)	0	6	0	9	X	
sp1 (not identified)	0	1	1	0	X	
Salticidae						
Beata sp.	0	1	0	7	X	
Chira sp1	0	2	0	0	X	

Table 2.—Continued.

Spiders	Number of individuals sampled per plant species				Guilds	
	NA	SA	EP	EA	WAN	WEB
Chira sp2						
sp1 (not identified)	0	0	0	7	X	
sp2 (not identified)	0	0	1	0	X	
sp3 (not identified)	0	0	1	0	X	
sp4 (not identified)	0	1	0	0	X	
sp5 (not identified)	0	1	0	0	X	
Tetragnathidae						
Leucauge sp.	0	0	4	6		X
Tetragnatha sp.	1	0	6	3		X
Theridiidae						
sp1 (not identified)	0	0	0	2		X
Theridiossomatidae						
Argyrodes sp.	0	0	1	1		X
Thomisidae						
Misumenops sp.	0	0	1	0	X	
Trechaleidae						
Paradossenus corumba Brescovit & Raizer	1	0	2	9	X	
Thaumasia sp.	1	3	10	11	X	
Total individuals	4	63	54	114	158	77
Total species	4	15	14	24	22	11
Number of samples	12	18	10	21		
Mean number of species ± SD	0.33 ± 0.65	3.50 ± 2.31	5.40 ± 4.30	5.43 ± 5.80	—	—
Species richness by rarefaction from 54 individuals ± SD	—	14.10 ± 0.84	14.00 ± 0.00	18.89 ± 1.56	—	—
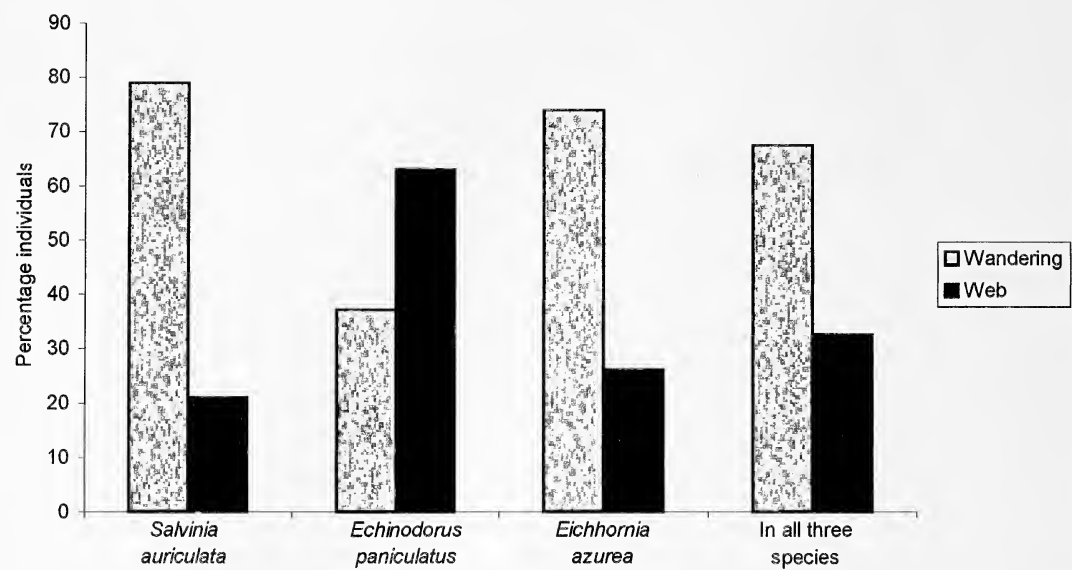
Figure 2.—Percentages of the numbers of individuals of each spider guild (wandering and web spiders) for the aquatic macrophytes analyzed (*Salvinia auriculata, Echinodorus paniculatus* and *Eichhornia azurea*).

among plants of different structural complexity classes, but also between those of the same class (*S. auriculata* and *E. paniculatus*). Differences between these two class-3 plants can be explained by the differences in height and density of their emersed parts. *Salvinia auriculata*, having high leaf density and small height above the water surface, favored the establishment of wandering spiders, which hunt and build their retreats on the leaves. Among the few web-weaving species found on this plant, only one, *Actinosoma pentacanthum* (Walckenaer, 1837), builds webs that are parallel to the water surface (Raizer 1997). This was actually the only spider seen employing the leaf mat of *S. auriculata* to attach a web with such orientation. On the other

hand, *E. paniculatus*, the macrophyte with the lowest leaf density and greatest height, favored the establishment of spiders that weave large-sized webs—such as those of the families Araneidae and Tetragnathidae. Similar results were found by Döbel et al. (1990) in a study on a community of spiders associated with the grass *Spartina alterniflora* Lois. This intertidal salt marsh plant presents three distinct habits: short, intermediate, and tall forms. The short form favors the occurrence of wandering spiders, while the intermediate one, with an architecture similar to that of *E. paniculatus*, enables the establishment of web-weaving species.

The variation in species composition among *E. azurea* (complexity class 4), *S. auriculata*

Table 3.—Mean proportion of spider species number per guild (web and wandering spiders) on *S. auriculata, E. paniculatus,* and *E. azurea.* Analysis of variance (ANOVA) was performed for the arc sine of the square root of the proportions of spider species per sample. On each line, values followed by the same letter do not differ significantly (Tukey test, $\alpha = 0.05$).

Guild	Salvinia auriculata (mean ± SD)	Echinodorus paniculatus (mean ± SD)	Eichhornia azurea (mean ± SD)	ANOVA results
web spiders	0.19 ± 0.22a	0.54 ± 0.31b	0.24 ± 0.26a	$F = 4.525$, df = 2, $P = 0.017$
wandering spiders	0.81 ± 0.22a	0.46 ± 0.31b	0.76 ± 0.26a	$F = 4.525$, df = 2, $P = 0.017$

and *E. paniculatus* (both of class 3) is possibly due to the number of spider species that are unique to *E. azurea* and to the small overlap of species composition between this plant and *E. paniculatus* (3 species in common) or *S. auriculata* (5 species in common). In addition, the proportion of web weavers occurring on *E. paniculatus* was higher than that of wandering spiders, whereas the opposite was observed for *S. auriculata* and *E. azurea* (Fig. 2). These data corroborate the results obtained by Hatley & MacMahon (1980) when comparing spider species compositions for bushes with differing leaf and branch densities. According to their findings, spider species that constructed large-sized webs were found in less structurally complex bushes with lower leaf and branch densities, but not in high-density plants. Our findings support the hypothesis that plants of different structural complexities favor distinct associations of spider species, thus influencing the species composition of such communities, as also found in other studies (e.g., Hatley & MacMahon 1980; Döbel et al. 1990, and Balfour & Rypstra 1998).

The expected number of spider species, as determined by rarefaction, varied among plant species. The greatest richness was the one recorded for the plant with the highest complexity class (*E. azurea*). However, no significant statistical difference was evidenced when richness was assessed by the mean number of spider species per sample, among plants.

Nonetheless, in a third analysis, when richness was assessed separately for each guild, the mean proportions between species numbers varied significantly (Table 3). *Echinodorus paniculatus* presented the highest proportion of web spider species, probably due to the dependence of such spiders on this plant's architecture, characterized by its high density and great height of leaves. On the other hand, the proportion of web spider species on *E. azurea* did not differ from that found for *S. auriculata*. This can be explained on the basis that orb-webs are usually anchored to open sites, which facilitate the capture of flying prey (insects). This feature would render the high leaf density of *E. azurea* unfavorable to the construction of such webs, which are mainly built on the edges of the patches formed by this plant (Raizer 1997). Nor does

S. auriculata offer suitable sites for the attachment of orb-webs, except those parallel to the water surface.

When wandering spiders alone were considered, *E. paniculatus* showed the smallest species richness, whereas *S. auriculata* and *E. azurea* did not differ from each other. As with web weavers, plant architecture can explain such results: *E. paniculatus* lacks a suitable architecture for the establishment of various species of wandering spiders since it never forms a mat on the water surface; *S. auriculata* and *E. azurea,* in turn, with their high leaf and branch densities, do form continuous mats that are rich in recesses and projections that favor wandering spiders.

The number of species of a given guild is thus influenced by variables of the structural complexity, such as the density and height of leaves and branches. In the present study, tall plants with low leaf densities displayed a larger number of web spider species, whereas a greater richness of wandering spiders was found for short plants with high leaf densities.

Our results support the hypothesis that structural complexity of plants also influences spider species richness, and corroborate other studies on the influence of habitat structure on species richness and species composition of spider assemblages (Hatley & MacMahon 1980; Greenstone 1984; Jennings & Hilburn 1988; Uetz 1991; Baur et al. 1996).

Habitat structural complexity is in fact one of the main factors used to explain species diversity (e.g., MacArthur & MacArthur 1961; Pianka 1978; Hatley & MacMahon 1980; Dean & Connell 1987; Shorrocks & Sevenster 1995). Magurran (1988) stated that habitats with high microsite diversity have greater species richness, since different microsites can have characteristic species associated with them. Other studies testing the relationship between structural complexity and species diversity have demonstrated that greater microsite diversity leads to a greater number of niches and can minimize interspecific competition (e.g., Pianka 1978; Hatley & MacMahon 1980; Shorrocks & Sevenster 1995). The present study has revealed that structurally dissimilar habitats may show similar spider species richnesses while differing in species composition. These findings support the suggestions of Jennings et al. (1988) and Baur et al. (1996) that communities of

spiders or other invertebrates are mainly organized as a function of the structural complexity of the environments.

Variations in species composition can be explained by habitat preferences resulting from behavioral and morphological characteristics of the spiders (Johnson 1995; Richman 1995).

Since richness of aquatic macrophyte species did not vary in the present investigation, remaining at value 1, it can be concluded that structural complexity is an important factor for the organization of spider communities on these plants, a factor that can affect richness and, even more strongly, composition of the spider species associated with them.

ACKNOWLEDGMENTS

LITERATURE CITED

Adámoli, J. 1982. O Pantanal e suas relações fitogeográficas com os cerrados. Anais do XXXII Congresso Nacional de Botânica 32:109–119.

Babcock, C.A. & C.R. Ely. 1994. Classification of vegetation communities in which geese rear broods on the Yukon-Kuskokwim delta, Alaska. Canadian Journal Botany 72:1294–1301.

Balfour, R.A. & A.L. Rypstra. 1998. The influence of habitat structure on spider density in a no-till soybean agroecosystem. Journal of Arachnology 26:221–226.

Baur, B., J. Joshi, B. Schmid, A. Hänggi, D. Borcard, J. Starý, A. Pedroli-Christen, G.H. Thommen, H. Luka, H. Rusterholz, P. Oggier, S. Ledergerber & A. Erhardt. 1996. Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. Revue Suisse Zoologie 103:801–833.

Boggiani, P.C. & A.M. Coimbra. 1996. A planície e os pantanais. Pp. 18–23. *In* Tuiuiú. Sob Os Céus Do Pantanal. Biologia E Conservação Do Tuiuiú (*Jabiru nycteria*) (P. T.Z. Antas & I.L.S. Nascimento, eds.). Empresa das Artes, São Paulo.

Brescovit, A.D., J. Raizer & M.E.C. Amaral. 2000. Descriptions and notes on the genus *Paradossenus* in the neotropical region (Araneae, Trechaleidae). Journal of Arachnology 28:7–15.

Cornell, H.V. & J.H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61:1–12.

Dean, R.L. & J.H. Connell. 1987. Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. Jounral of Experimental Marine Biology and Ecology 109:217–247.

Döbel, H.G., R.F. Denno & J.A. Coddington. 1990. Spider (Araneae) community structure in an intertidal salt marsh: Effects of vegetation structure and tidal flooding. Environmental Entomology 19:1357–1370.

Dueser, R.D. & J.H. Porter. 1986. Habitat use by insular small mammals: Relative effects of competition and habitat structure. Ecology 67:195–201.

Greenstone, M.H. 1984. Determinants of web spider species diversity: Vegetation structural diversity vs. prey availability. Oecologia (Heidelberg) 62:299–304.

Gunnarsson, B. 1988. Spruce-living spiders and forest decline; the importance of needle loss. Biological Conservation 43:309–319.

Gunnarsson, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. Journal of Animal Ecology 59:743–752.

Hatley, C.L. & J.A. MacMahon. 1980. Spider community organization: Seasonal variation and the role of vegetation architecture. Environmental Entomology 9:632–639.

Heckman, C.W. 1994. New limnological nomenclature to describe ecosystem structure in the tropical wet-and-dry climatic zone. Archiv fuer Hydrobiologie 130:385–407.

Jennings, D.T. & D.J. Hilburn. 1988. Spiders (Araneae) captured in malaise traps in spruce-fir forests of west-central Maine. Journal of Arachnology 16:85–94.

Jennings, D.T., M.W. Houseweart, C.D. Dondale & J.H. Redner. 1988. Spiders (Araneae) associated with strip-clearcut and dense spruce-fir forests of Maine. Journal of Arachnology 16:55–70.

Johnson, S.R. 1995. Observation of habitat use by *Sarinda hentzi* (Araneae, Salticidae) in northeastern Kansas. Journal of Arachnology 23:71–74.

Krebs, C.J. 1989. Ecological Methodology. Harper & Row, New York.

MacArthur, R.H. & J.W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Magurran, A.E. 1988. Ecological Diversity And Its Measurement. Chapman and Hall, New York.

Merck, A.M.T. 1988. A fauna do pleuston *Salvinia auriculata* Aublet (Pteridophyta, Salviniaceae) do Lago Barigui, Curitiba, Paraná. I. Flutuação anual da densidade. Revista Brasiliera de Biologia 48:991–1004.

Murdock, W.W., F.C. Evans & C.H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology 53:819–829.

Pearsons, T.N., H.W. Li & G.A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society 121:427–436.

Pianka, E.R. 1966. Convexity, desert lizards, and spatial heterogeneity. Ecology 47:1055–1059.

Pianka, E.R. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333–351.

Pianka, E.R. 1978. Evolutionary Ecology. Harper & Row, New York.

Pulz, R. 1987. Thermal and water relations. Pp. 26–55. *In* Ecophysiology Of Spiders (W. Nentwig, ed.). Springer-Verlag, Berlin.

Raizer, J. 1997. Spiders Associated With Aquatic Macrophytes In The Pantanal of Mato Grosso Do Sul State. MS Thesis, Universidade Federal de Mato Grosso do Sul. 41 pp. (in Portuguese)

Richman, D.B. 1995. A comparison of populations of wolf spiders (Araneae, Lycosidae) on two different substrates in southern Florida. Journal of Arachnology 23:151–156.

Robinson, J.V. 1981. The effect of architectural variation in habitat on a spider community: An experimental field study. Ecology 62:73–80.

Shorrocks, B. & J.G. Sevenster. 1995. Explaining local species diversity. Proceedings of the Royal Society of London, B. Biological Sciences 260:305–309.

Uetz, G.W. 1975. Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. Environmental Entomology 4:719–724.

Uetz, G.W. 1977. Coexistence in a guild of wandering spiders. Journal of Animal Ecology 46:531–541.

Uetz, G.W. 1991. Habitat structure and spider foraging. Pp. 325–348. *In* Habitat Structure. The Physical Arrangement of Objects in Space (S.S. Bell, E.D. McCoy & H.R. Mushinsky, eds.). Chapman and Hall, London.

ON THE DISTRIBUTION AND PHENOLOGY OF *ARGYRODES FICTILIUM* (ARANEAE, THERIDIIDAE) AT ITS NORTHERN LIMIT OF NORTH AMERICA

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ABSTRACT. *Argyrodes fictilium* is a rarely collected species whose northern range was thought to be southern Canada. Recent collections in the eastern boreal forests of Québec extend its distribution range to the north and suggest that *A. fictilium* might be found anywhere within the boreal forest tree limit. Mature males collected in May indicate a summer-stenochronous type of phenology.

Keywords: Distribution, phenology, boreal, araneophagic

The genus *Argyrodes* Simon 1864 is known in Canada from three species easily recognizable as members of the genus by their unusual triangular abdomen (Exline & Levi 1962). These are *Argyrodes trigonum* (Hentz 1850), *A. cancellatus* (Hentz 1850) and *Argyrodes fictilium* (Hentz 1850). The elongated palpal tibia and femur of *A. fictilium* are peculiar, but the male and female genitalia leave no doubt about the species' identity nor its generic affinity. According to Exline & Levi (1962), this species is rare but ranges from southern Canada to Panama. In a recent revision of the Neotropical species of the genus, Gonzàlez & Castro (1996) confirmed the distributional pattern of *A. fictilium*, including its southern Canadian localities and its presence in South America with new records from Argentina.

We present new data concerning the distribution and phenology of *A. fictilium* at its northern limit and provide a new illustration of the male palp. The data (Table 1) used to build the distribution map and the phenology graph were gathered from three sources: literature, private and public collections, and our own collection. Genitalia of available specimens were studied with a Nikon SMZ-U, and Fig. 1 was done with a camera lucida and a hybrid technique of traditional line drawing with India Ink and computer drawing on Macintosh.

Males of almost all American species of the genus *Argyrodes*, except for *A. fictilium*, have a cephalic projection or protuberance which is characterized by an unmodified, rather flat cephalothorax (Exline & Levi 1962). The genitalia of Québec and Ontario specimens were studied (Fig. 1) and the specimens from Canada are identical to those occurring from the United States (Exline & Levi 1962) to Argentina, including Cuba and Jamaica (Gonzàlez & Castro 1996).

While the genus *Argyrodes* is well known for its peculiar kleptoparasitic feeding habits (Tanaka 1984; Whitehouse 1988, 1997), *A. fictilium* has been reported to prey on *Araneus* sp., *Frontinella communis* (Hentz 1850), *Philoponella oweni* (Chamberlin 1924), *Frontinella* sp. and an unidentified linyphiid (Archer 1946; Exline & Levi 1962; Trail 1981; W. Shear pers. comm.). Trail (1981) has suggested that large *Argyrodes* species prey on other spiders while smaller species are kleptoparasites, but Tanaka (1984) showed that small *Argyrodes* also prey on big spider species. Present knowledge suggests that all species studied so far in the *Rhomphaea* species group, including *A. fictilium*, are araneophagic rather than kleptoparasites (Archer 1940; Whitehouse 1987, pers. comm.).

The distribution map (Fig. 2) confirms the wide and scattered distribution of the species at its northern limit, with records from the eastern and western regions of Canada. In Exline & Levi (1962) and Gonzàlez & Castro (1996), the northern limit "southern Canada" referred to the records from Vancouver Island (British Columbia) and Lake Temagami (On-

Figure 1.—*Argyrodes fictilium* from Nouveau-Québec Territories (49°48′N, 78°54′W) Québec, palpus, ventral view.

tario). Some new records presented here show a much more northerly distribution than previously reported. In particular, the records of Paquin and Dupérré (Table 1) in the black spruce forest of eastern Canada and the one by Aitchison-Benell & Dondale (1992) in Manitoba extend the species' distribution to the boreal region.

Two hypotheses are formulated here concerning the distribution of *A. fictilium* in the boreal region, this species being of a Neotropical origin (Gonzàlez & Castro 1996). The first explains the northern distribution as the sporadic northern extension of a species usually confined to more southern latitudes. On a smaller geographical scale, the variability of environmental conditions such as temperature and moisture would allow its sporadic presence in more northern latitudes. The instability of such conditions would explain its rarity as well as the gaps in its distribution in the boreal area. An example of such a dynamic is given by *Neochlamisus comptoniae* (Brown) (Coleoptera, Chrysomelidae), an insect that is known to have a northern limit around the U.S. and Canada border (LeSage 1984) while its host plant, *Comptonia peregrina* (L.) Coulter, is present in northern Québec (Marie-Victorin 1964).

The second hypothesis states that the distribution of *A. fictilium* may also include the boreal region, which is delimited by the north-
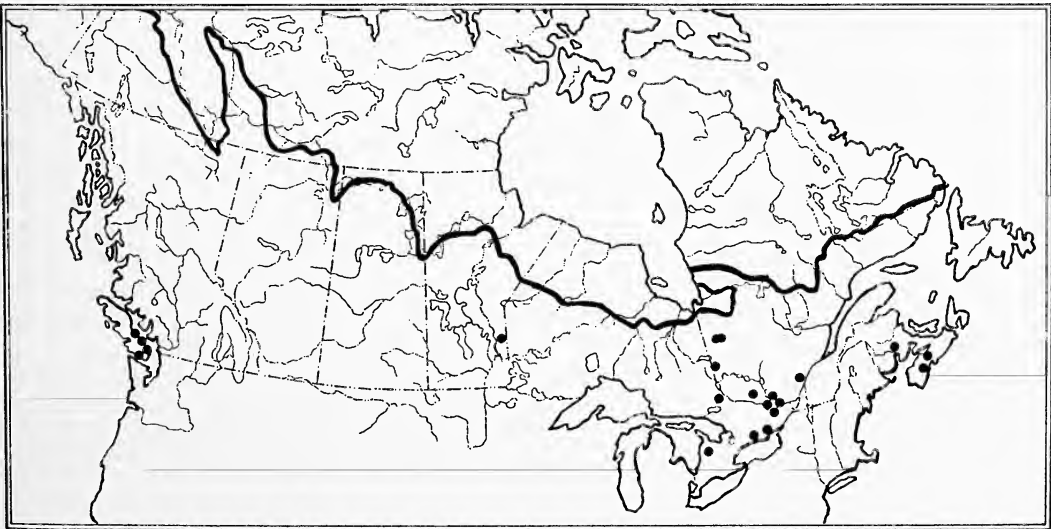

Figure 2.—Distribution of *Argyrodes fictilium* in Canada. The solid line shows the northern limit of the boreal forest.

Table 1.—Collection data from collections and literature. (CNC: Canada National Collection, DBC: Donald J. Buckle Collection, LLC: Laurent LeSage Collection, CPAD Pierre Paquin and Nadine Dupérré Collection).

Data source	Province and locality	Date of collection	Sex	Notes
From collections				
CNC	BRITISH COLUM-BIA: Qualicum beach	23 May 1946	2 F	—
CNC	NOVA SCOTIA: Ca-nard	05 Sept. 1956	M	Apple trees
CNC	ONTARIO: Odessa	04 July 1963	F	—
CNC	ONTARIO: Belleville (Field station)	09 June 1960	F	Pine
CNC	NEW BRUNSWICK: Fredericton	02–03 July 1969	F	Balsam fir
CNC	ONTARIO: Markdale	17 June 1988	F	Cedar fen beating
CNC	ONTARIO: Ottawa	03–09 July 1989	M	Damp acer/betula wood
DBC	NOVA SCOTIA: Ma-hone Bay	24 Sept. 1996	Juv.	Balsam fir
LLC	QUÉBEC: Pontiac, Lake Davis (N of Fort-Coulonge)	24 August 1991	Juv.	Mixed forest, beating
LLC	QUÉBEC: Pontiac; Lake Davis (N of Fort-Coulonge)	01 Sept. 1990	Juv.	Mixed forest, beating
CPAD	QUÉBEC: Nouveau-Québec Territories; 49°48′N, 78°54′W	06–13 July 1997	M	Burned Black spruce forest, flight inter-ception trap
CPAD	QUÉBEC: Nouveau-Québec Territories; 49°48′N, 78°54′W	29 June–6 July 1997	M	Mature Black spruce forest, flight inter-ception trap
CPAD	QUÉBEC: Abitibi; Lake Duparquet; 48°30′N, 79°13′W	24–30 June 1997	M	Mature Jackpine forest, soil emerging cage
From literature				
Emerton (1920)	QUÉBEC: Outaouais; Hull	—	—	—
Kurata (1943)	ONTARIO: Nipissing Co.; Lake Temagami	20 August 1937	F	—
Exline & Levi (1962)	ONTARIO: Nipissing Co.; Lake Temagami	—	—	—
	BRITISH COLUMBIA: Pender Harbour	—	—	—
	BRITISH COLUMBIA: Wel-lington	—	—	—
	BRITISH COLUMBIA: Nanai-mo	—	—	—
Aitchison-Bennel & Dondale (1992)	MANITOBA: 51°30′N, 95°00′W (C4)	—	—	Boreal forest; decidous woods; tree foliage

Table 1.—Continued.

Data source	Province and locality	Date of collection	Sex	Notes
LeSage & Hutch-inson (1992)	QUÉBEC: Maski-nongé; St-Angèle	12 July 1990	Juv.	Mixed forest, beating
	QUÉBEC: Gatineau; Aylmer	08 Sept. 1990	Juv.	Maple-beech forest, beating
	QUÉBEC: Pontiac; Lake Davis (N of Fort-Coulonge)	01 Sept. 1990	Juv.	Mixed forest, beating
	QUÉBEC: Pontiac; Lake Davis (N of Fort-Coulonge)	30 Sept. 1990	6 Juv.	Mixed forest, beating

ern tree limit (Danks & Footitt 1989) (Fig. 2). This hypothesis partially relies on the records of Aitchison-Benell & Dondale (1992) from Manitoba, and Paquin and Dupérré (Table 1) from Québec, both from the boreal region but in two different ecological contexts. As mentioned by Scudder (1979), the boreal ecological zone forms a vast transcontinental belt and the largest continuous vegetation association in North America. This wide ecological zone is roughly divided into a southern and a northern part. The southern part (also called mixed-boreal) is dominated by deciduous (aspen and birch) and coniferous forest (white spruce, balsam fir, and white cedar) while the northern part is mainly dominated by black spruce (Grandtner 1966; Rowe 1972). In eastern Canada, the boreal belt is under the strong climatic influence of Hudson and James Bays. In this area, northern conditions are met at a lower latitude than anywhere else in the country (Danks 1979). This distribution pattern is shown by the black spruce distribution across Canada (Rowes 1972).

Very little is known about the biological traits of *A. fictilium* and its ecological preferences. Its distribution pattern might, however, reflect a wide range of potential prey rather than a limited distribution of a specific host. The known prey of *A. fictilium* are likely to find suitable web substrate everywhere within the tree limit; and the records of *A. fictilium* indicate an association with forest habitats, particularly coniferous forest (Table 1). This suggests that food would not be a limiting factor. Other abiotic factors that might limit its northern distribution are largely unknown.

There is little evidence to favor either of the two hypotheses for the distribution of *A. fic-*

tilium. Nevertheless, the hypothesis for a distribution that covers the boreal area rather then a sporadic extension seems to be better supported when the records from Québec are considered. Even though the record of *A. fictilium* from Manitoba is the most northern for the species in regards to the latitude, it does not indicate an extension of the species range into the northern boreal region because it is reported from the mixed-boreal forest. However, the records from the black spruce forest of Québec allow such a range extension into the northern boreal area. Despite the lower latitudes of the localities, these records come from an ecological zone that is more representative of northern conditions as shown by the vegetation belt and climatic data (Danks 1979). The presence of *A. fictilium* in the black spruce forests of Québec clearly indicate that the species occurs in the northern boreal area; and, according to the second hypothesis, its presence can be expected throughout this wide ecological region.

Figure 3 shows periods of collection for the known Canadian specimens of *A. fictilium*. Mature females are active from the end of May until the beginning of July while males seem to appear later in the season, from the end of June until September. Juveniles are mainly reported in September, and we assume these to be the overwintering stages. According to Tretzel (1954) there are three types of phenology: 1) stenochronous where adults are present in a definite period of the year, 2) eurychronous where adults are present all year long (with or without a definite reproduction period), and 3) winter-mature. The male peak of abundance is considered to be the indicator of the maturation period. Aitchison (1984),
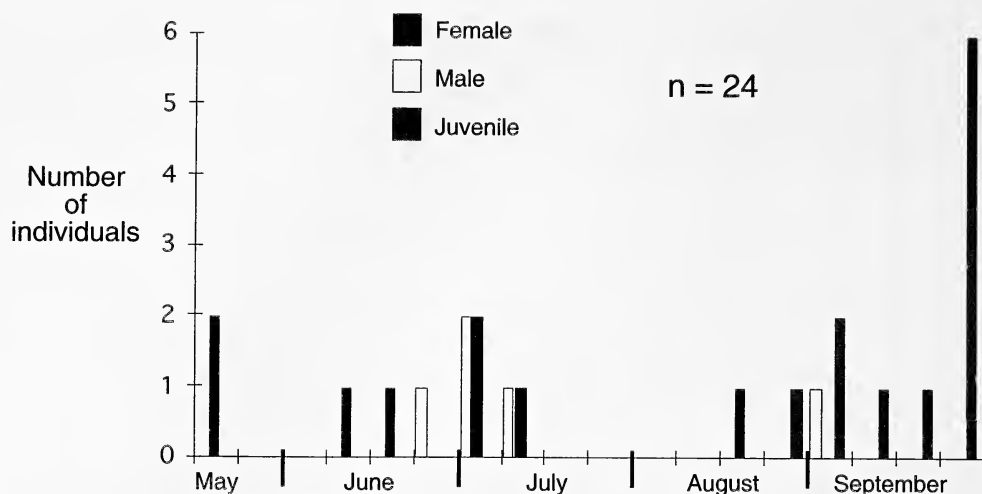
Figure 3.—Seasonal distribution of immature, male, and female of *Argyrodes fictilium* in Canada.

however, refined that terminology by dividing the stenochronous type into three classes: spring-, summer- and autumn-stenochronous. Despite the fact that it is difficult to confirm a phenological type with so few specimens, the summer-stenochronous class fits our data, mature males being collected mainly in July.

Argyrodes fictilium is a rare species within its northern limits and it is difficult to study its biology. Only 30 specimens are known from Canada, most of them from Québec and Ontario where the collection intensity may have been higher than in other parts of the country. It is also difficult to see a clear pattern in its distribution because of the rarity of the species and the lack of collections. However, the present state of knowledge allows a hypothesis that may link the forested portion of the territory to its distribution, including the boreal forest. It is surprising to see a species with such wide range of habitat occurring from South America to the boreal forest. Future collections, especially in poorly studied regions such as the northern boreal forest in central and western part of Canada, are likely to yield more specimens and confirm its phenology and distributional pattern.

ACKNOWLEDGMENTS

LITERATURE CITED

Aitchison, C.W. 1984. The phenology of winter-active spiders. Journal of Arachnology 12:249–271.

Aitchison-Benell, C.W. & C.D. Dondale. 1992 (1990). A checklist of Manitoba spiders (Araneae) with notes on geographic relationships. Naturaliste Canadien 117:215–237.

Archer, A.F. 1940. The Argiopidae or orb-weaving spiders of Alabama. Alabama Museum of Natural History, paper 14:1–77.

Archer, A.F. 1946. The Theridiidae or comb-footed spiders of Alabama. Alabama Museum of Natural History, paper 22:1–67.

Danks, H.V. 1979. Physical basis for Canadian regional diversity. Pp. 7–30. *In* Canada and Its Insect Fauna (H.V. Danks, ed.). Memoirs of the Entomological Society of Canada, No. 108.

Danks, H.V. & R.G. Footitt. 1989. Insects of the boreal zone of Canada. Canadian Entomologist 121:625–690.

Emerton, J.H. 1920. Catalogue of the spiders of Canada known to the year 1919. Transactions of the Royal Canadian Institute 12:309–338.

Exline, H. & H.W. Levi. 1962. American spiders of the genus *Argyrodes* (Araneae: Theridiidae). Bulletin of the Museum of Comparative Zoology 127:75–204.

González, A. & D. del C. Castro. 1996. Neotropical spiders of the genus *Argyrodes* Simon (Araneae, Theridiidae). Bulletin of the British Arachnological Society 10:127–137.

Grandtner, M.M. 1966. La végétation forestière du Québec méridional. Les Presse de l'Université Laval, Québec, Canada. 216 pp.

Kurata, T.B. 1943. The spiders of the Lake Nipissing and Lake Temagami regions, Ontario. Canadian Field Naturalist 57:9–13.

LeSage, L. 1984. Immature stages of Canadian *Neochlamisus* Karren (Coleoptera: Chrysomelidae). Canadian Entomologist 116:383–409.

LeSage, L. & R. Hutchinson. 1992. Une des plus extraordinaires araignées du Québec *Argyrodes fictilium* (Hentz) (Araneae: Theridiidae). Pirata 1: 127–129.

Marie-Victorin. 1964. La Flore Laurentienne. 2ème Édition. Les Presses de l'université de Montréal, Montréal. 925 pp.

Rowe, R.S. 1972. Forest Region of Canada. Environment Canada. Publ. No. 1300. Ottawa, Ontario, Canada. 172 pp.

Scudder, G.G.E. 1979. Present patterns in the fauna and flora of Canada. Pp. 87–179. *In* Canada and Its Insect Fauna (H.V. Danks, ed.). Memoirs of the Entomological Society of Canada, No. 108.

Trail, D.S. 1981 (1980). Predation by *Argyrodes* (Theridiidae) on solitary and communal spiders. Psyche 87:349–355.

Tanaka, K. 1984. Rate of predation by a klepto-parasitic spider, *Argyrodes fissifrons* upon a large host spider, *Agelena limbata*. Journal of Arachnology 12:363–367.

Tretzel, E. von. 1954. Reife- und Fortpflanzungszeit bei Spinnen. Zeitschrift fuer Morphologie und Ökologie der Tiere 42:634–691.

Whitehouse, M.A.E. 1987. Spider eat spider: The predatory behaviour of *Rhomphaea* sp. indet. from New Zealand. Journal of Arachnology 15: 355–362.

Whitehouse, M.A.E. 1988. Factors influencing specificity and choice of host in *Argyrodes antipodiana* (Theridiidae). Journal of Arachnology 16:349–355.

Whitehouse, M.A.E. 1997. The benefits of stealing from a predator: Foraging rates, predation risk and intraspecific aggression in the kleptoparasitic spider *Argyrodes antipodiana*. Behavioral Ecology 8:663–667.

EGG SAC RECOGNITION BY FEMALE
MIAGRAMMOPES ANIMOTUS (ARANEAE, ULOBORIDAE)

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ABSTRACT. After producing a cylindrical egg sac, a female *Miagrammopes animotus* holds it until spiderlings emerge and disperse. When sacs were taken from females, these females exhibited a putative searching behavior and, upon contacting either their sacs or those of conspecifics, exhibited a putative recognition behavior. These responses would cause a female to search for and reclaim her sac if it were temporarily abandoned during feeding or web construction. Females with sacs did not respond positively to sacs from which spiderlings had emerged. Females that did not have sacs did not respond positively to viable sacs. Females separated from their sacs for increasing time periods exhibited a decline in positive responses to their sacs. Thus, contact with the sac appears necessary to maintain an affinity for the sac during the development of spiderlings.

Keywords: Maternal care, spider

Females of the simple-web species *Miagrammopes animotus* Chickering 1968 produce cylindrical egg sacs consisting of two columns of eggs surrounded by two thin layers of silk (Lubin et al. 1978; Opell 1984). During the day, a female attaches her egg sac along one of the web's non-sticky lines and aligns herself with the egg sac, her abdomen touching the egg sac, her legs I and II extending directly anteriorly, and her legs III and IV extending directly posteriorly (Fig. 1; Lubin et al. 1978; Opell 1989a). This posture enhances the twig-like appearance of both the female and her egg sac. *Miagrammopes animotus* females range in color from light tan to dark, reddish-brown and produce egg sacs whose wrapping silk is similar in color to their bodies (Opell 1989a). This makes it even more difficult to distinguish a spider and her egg sac and further enhances the cryptic appearance of each.

At dusk a female detaches her egg sac from the line and holds the sac with her first leg as she monitors her web (Fig. 2; Lubin et al. 1978; Opell unpubl. obs.). This suggests that her linear, day-time posture is a defense against visually hunting predators like insects and birds. When spiderlings emerge from an egg sac as second instars, they lack functional cribella and cling to the egg sac for several days until they molt to the third instar (Lubin et al. 1978; Opell 1989b), at which time they

disperse and begin constructing capture webs. Females continue to tend their egg sacs until spiderlings leave (Fig. 3).

While collecting *M. animotus* in conjunction with studies of their cribellar threads and cribella, I routinely collected females with egg sacs. When I attempted to remove a female's egg sac so that I could weigh and measure her, she held tenaciously to her egg sac. Unless all of her legs were removed from the egg sac, she quickly regained her firm grasp. After I separated a female from her egg sac and placed her on a horizontal surface, she walked rapidly and made broad, rapid sweeping movements with her first legs. When she contacted her egg sac, she held it tightly with her first two pairs of legs, immediately pressed her chelicerae to its surface for a few seconds (although I could not determine if she bit the egg sac's silk covering), and then immediately firmly grasped the egg sac with her first and second legs. When a female with an egg sac was placed on a horizontal surface, she often attached a dragline to her egg sac and walked away, possibly searching for a secure site to climb. When either the egg sac or dragline was touched, the female ran quickly to her egg sac, pressed her chelicerae to its surface and then grasped the egg sac.

I interpreted this rapid walking and leg waving behavior as searching behavior, the cheliceral contact as egg sac evaluation be-
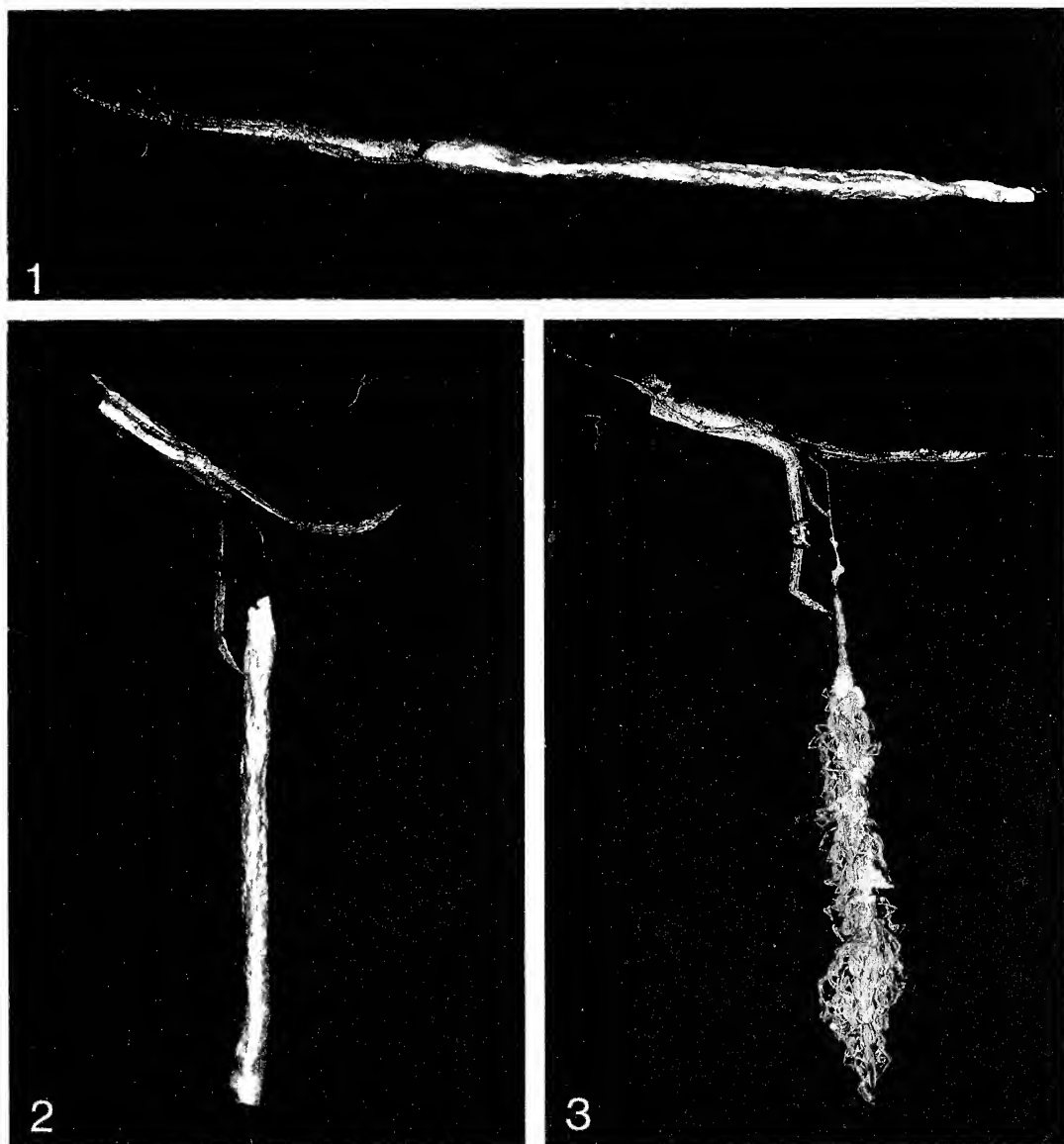
Figures 1–3.—*Miagrammopes animotus* females tending egg sacs during the day (1), at night (2), and after spiderlings have emerged (3).

havior, and the subsequent grasping of the egg sac as positive egg sac recognition. To better understand this behavior, I evaluated the responses of females that had no egg sacs, investigated the specificity of egg sac recognition, and determined if this behavior was expressed after a female had been separated from her egg sac for different lengths of time.

METHODS

Spiders and egg sacs were collected at the Center for Energy and Environment Re-

search's El Verde, Puerto Rico field station. Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology. All observations were made in a windowless laboratory that was illuminated by fluorescent lights and had a temperature of 20–24 °C and a relative humidity of 60–63%.

After removing a female's egg sac, I placed each in a separate, clean glass vial stoppered with a cotton plug. A small piece of moist cotton was placed with each spider. Vials were numbered so that I could identify each spi-

der's egg sac, though only by referring to a record book. Observations were conducted by placing a female in a clean, 40 mm diameter aluminum weighing pan and observing her response to an object or an egg sac. I define a positive response to an object or an egg sac as the female clinging tightly to the object after contacting it with her chelicerae so that she could not be easily dislodged by repeated prodding with a small artist's brush. Occasionally, a female rested momentarily on an egg sac or object, but did not bring her chelicerae to its surface. In these cases a light prod with a brush caused her to leave the object and continue walking and I scored this as a negative response.

I examined the duration of egg sac recognition in 82 females that were collected with egg sacs. After removing their egg sacs, I kept these spiders for periods of 5–25 h. At the end of each of these 21 periods the responses of 2–10 females to their own egg sacs were observed. Thirty-four of the females that responded positively to their egg sacs were used for a second trial after each was kept in a vial with her egg sac for 12–24 h to permit prolonged contact with her sac.

RESULTS

Eleven mature females that had no egg sacs, including five whose abdomens were clearly swollen with eggs, did not cling to egg sacs or press their chelicerae to their surfaces when each was presented with 7–10 egg sacs of conspecifics, nor did they cling tightly to pieces of grass or cotton that I placed in their collecting vials. In contrast, 26 of 32 females whose egg sacs were removed 5–6 h earlier responded positively to their reintroduced egg sacs. The response of each group differed from a null model in which 50% of the individuals responded positively to egg sacs (χ^2 = 11.0 and 12.5, respectively, $P < 0.001$).

Two females that responded positively to their own egg sacs also responded positively to egg sacs produced by nine other females. Seven females that responded positively to their own egg sacs also responded positively to an egg sac of the closely related species *M. pinopus* Chickering 1968 from St. John, U.S. Virgin Islands. However, they did not respond positively to a piece of cotton, a section of wooden applicator stick similar in size to an egg sac, or to an egg sac of *Uloborus glo-*

mosus (Walckenaer 1841) from Blacksburg, Virginia. Another five females that responded positively to egg sacs that contained eggs responded negatively to egg sacs from which spiderlings had emerged, walking over these egg sacs and continuing to exhibit searching behavior.

Figure 4 shows the percentages of females that responded positively to their egg sacs after times of increasing separation. In each of the first six time intervals, the responses of females used in a second trial did not differ from that of females that were used in only one trial ($\chi^2 < 0.425$, 1 df, $P > 0.50$). However, in the last interval (23–25 h) five of the six females used in a second trial responded positively to their egg sacs, a greater number than predicted by the responses of females used in only one trial ($\chi^2 = 16.000$, 1 df, $P < 0.001$). The median time of these seven periods regresses against the percent positive response (Y = -2.06X + 92.92; F = 8.20, P = 0.035, R^2 = 0.62), indicating that a female's ability to identify and respond to her egg sac decays with increasing separation. Additional support for this decay comes from a comparison of the responses when grouped into short, intermediate, and long periods of egg sac separation (5–9 h, n = 35; 10–20 h, n = 48; and 21–25 h, n = 33; respectively). For this comparison, I determined the mean positive response for each of the 21 hourly trials and then compared the grand means of responses in the three periods. A Kruskal-Wallis test showed that the values of these periods (X ± 1 SD: 78.7% ± 19.7, 66.0% ± 27.4, and 38.9% ± 7.9, respectively) differed (χ^2 = 6.47, P = 0.039).

DISCUSSION

These observations indicate that sensory stimuli from one or several sources unique to oviposition or egg sac construction cause persistent but reversible changes in a spider's physiology that alter its response to egg sacs. Possible sources of these stimuli include the pressure exerted on the oviducts as eggs pass through them and the activation of tubuliform silk glands and spigots that, in uloborids, appear to be used only for egg sac production (Kovoor 1977; Foelix 1996; Opell 1984). Copulation is an unlikely source of stimuli, as females store sperm and mating may occur long before eggs are fertilized and deposited.
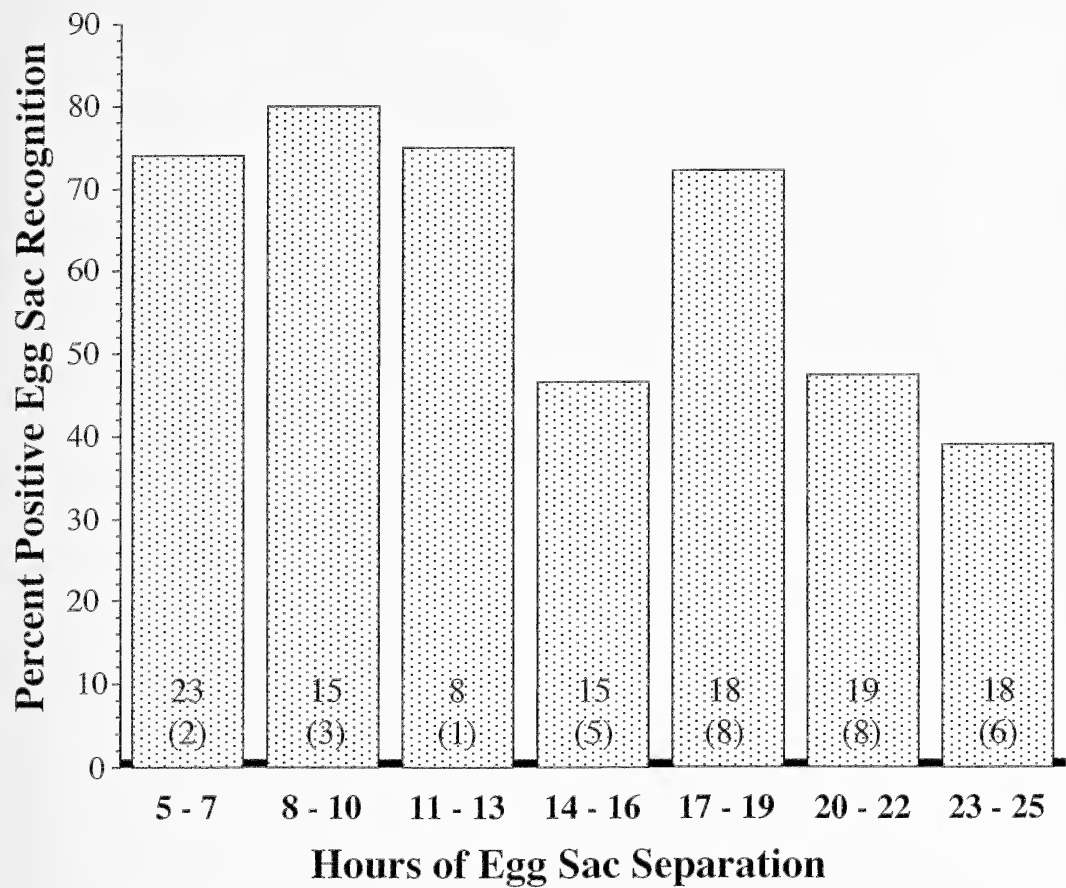
Figure 4.—Positive egg sac recognition following periods of increasing separation of a female and her egg sac. Bars represent the means of the three-hour periods. The sample size is given within each bar. The number of females used in a second trial is given in parentheses.

Once a positive response to an egg sac has been established it appears to be general and does not permit a female to distinguish her egg sac from those of conspecifics. However, unlike wolf and fishing spiders, *M. animotus* females can not be tricked into accepting substitute objects (Gertsch 1979; Foelix 1996). Egg sac recognition persists for varying periods of time, but lasts long enough to cause a female to search thoroughly for her egg sac if she left it. The regression formula for the decay of positive responses to egg sacs suggests that egg sac recognition disappears in all females after they are separated from their egg sacs for about 45 h. Continual or frequent contact with an egg sac appears to be necessary to maintain a female's positive response to her egg sac during the approximately 20 days required for the eggs to develop and the spider-

lings to emerge from the egg sac (Opell 1979, 1982; Peaslee & Peck 1983).

Unlike members of other uloborid genera, *Miagrammopes* females have no permanent attachment site for their egg sacs. At night females probably temporarily attach the egg sac to a line while renewing their capture webs and feeding. This behavior has not been observed in *M. animotus*; but Lubin et al. (1978) report that females of an unidentified *Miagrammopes* species hung their egg sacs from threads at night and resumed prey capture activity until dawn, at which time they again tended their egg sacs. Egg sac recognition would cause a female to search for her egg sac if she were forced to abandon it during the day or to anchor it while building or repairing her capture web at night.

I did not investigate cues that might permit

females to distinguish viable egg sacs from those that the young have abandoned. The masses of viable and empty egg sacs differ; but, in my laboratory observations, females did not appear to lift egg sacs to assess their masses. Second instar spiderlings may deposit silk on the egg sac's outer surface and this may mask the egg sac silk that allows a female to identify an egg sac. Alternatively, the female may identify and respond negatively to the silk of these spiderlings.

The loss of egg sac recognition has advantages for *M. animotus* females that appear to produce several egg sacs during a lifetime and often reach high densities. A female's negative response to an egg sac from which spiderlings have emerged and dispersed allows her to shift her activity from egg sac tending to web building and foraging so that another egg sac can be produced. This negative response may also reduce intraspecific conflict. At El Verde, I often observed 3–5 mature females on a single under-story plant or cluster of vegetation occupying a space of about 1 m^3. Under these high densities, the loss of egg sac recognition would eliminate contests between females that were tending egg sacs and those from whose egg sacs spiderlings had recently dispersed. In the absence of individual-specific egg sac recognition, the failure of females to respond to old egg sacs also assures that they will not mistakenly abandon viable egg sacs for these discarded egg sacs that sometimes remain suspended from vegetation.

LITERATURE CITED

Foelix, R.G. 1996. Biology of Spiders. 2nd ed. Oxford Univ. Press, New York.

Gertsch, W.J. 1979. American Spiders. Van Nostrand Company, Inc., New York.

Kovoor. J. 1977. L'appareil sericignene dans le genera *Uloborus* Latr. (Araneae, Uloboridae). I. Anatomic Revue Arachnologique 1:89–102.

Lubin, Y.D., W.G. Eberhard & G.G. Montgomery. 1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche 85:1–23.

Opell, B.D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bulletin of the Museum of Comparative Zoology 148:433–549.

Opell, B.D. 1982. Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae, Uloboridae). Journal of Arachnology 10:185–191.

Opell, B.D. 1984. Eggsac differences in the spider family Uloboridae (Arachnida: Araneae). Transactions of the American Microscopical Society 103:122–129.

Opell, B.D. 1989a. Do female *Miagrammopes animotus* (Araneae: Uloboridae) spin color-coordinated egg sacs. Journal of Arachnology 17:108–111.

Opell, B.D. 1989b. Functional associations between the cribellum spinning plate and prey capture threads of *Miagrammopes animotus* (Araneida, Uloboridae). Zoomorphology 108:263–267.

Peaslee, J.E. & W.B. Peck. 1983. The biology of *Octonoba octonaria* (Muma) (Araneae, Uloboridae). Journal of Arachnology 11:51–67.

EGG COVERING BEHAVIOR OF THE NEOTROPICAL HARVESTMAN *PROMITOBATES ORNATUS* (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. The egg covering behavior of the laniatorid harvestman *Promitobates ornatus* was studied. Females of this species laid eggs isolated, on soil. After laying an egg, the female started scraping the substrate next to the egg, picking up debris, and attached the earth particles to the egg. After she scraped one area, she rotated around the egg, stopped turning, and restarted the collection of debris from another site. Alternation of scraping and changing body position was repeated twice or more until the female completed the egg covering. Data on egg size, duration of egg laying and egg covering, and duration of embryonic development are also provided.

Keywords: Laniatores, Mitobatinae, biology, care, maternal investment

In the Laniatorine suborder of Opiliones, females lay eggs that are either clustered (Canals 1936; Capocasale & Bruno-Trezza 1964; Mitchell 1971; Juberthie & Muñoz-Cuevas 1971; Matthiesen 1975; Goodnight & Goodnight 1976; Pinto-da-Rocha 1993; Ramires & Giaretta 1994; Gnaspini 1995; Machado & Oliveira 1998) or isolated (Canals 1936; Juberthie 1965, 1972; Cokendolpher & Jones 1991), on a large variety of substrates, such as leaves, moss, rocks, bark crevices and soil.

Among the Laniatores (unless otherwise indicated, all species mentioned below belong to the family Gonyleptidae), different forms of parental investment have been described in the literature, ranging from the oviposition site selection to egg guarding. Egg guarding has been observed in one species of Cosmetidae and one of Stynopsidae and in seven species of Gonyleptidae (see Gnaspini 1995 for references), and is usually performed by females. Paternal care has seldom been reported (Rodriguez & Guerrero 1976; Mora 1990; Martens 1993) and there is no record of biparental care in harvestmen, although Machado & Oliveira (1998) reported males of *Goniosoma longipes* (Roewer 1913) near the eggs, and taking care of eggs when the female was experimentally removed.

Scotolemon lespesi Lucas 1860 (Juberthie 1965), *Cynorta cubana* (Banks 1909) (Cosmetidae) (Juberthie 1972), *Pachylus quinamavidensis* Muñoz-Cuevas 1969 (Juberthie &

Muñoz-Cuevas 1971), *Vonones sayi* (Simon 1879) (Cosmetidae) (Cokendolpher & Jones 1991) as well as two other species of cosmetids and six species of gonyleptids (Canals 1936) are known to cover eggs with debris.

The behavior of covering eggs has never been described in detail. The only mention of how egg covering occurs was by Canals (1936), who reported "scraping of the substrate with the anterior legs" by the female. Again, he did not specify which species did this. This paper provides the first detailed description of egg covering behavior in harvestmen, based on data from *Promitobates ornatus* (Mello-Leitão 1922) (Mitobatinae).

Three female *P. ornatus* were used for this study. One of them (identified as *Po*1) was collected on 24 January 1999 in Carlos Botelho State Park, São Miguel Arcanjo county. The other two (identified as *Po*2 and *Po*3) were collected on 27 July 1999 in Paranapiacaba (= Alto da Serra), Santo André county. Both localities are representative of tropical rain forest in São Paulo state, southeastern Brazil. I maintained *Po*1 with a conspecific male at room temperature in a terrarium with damp soil, a wet piece of cotton, and hard surfaces such as stones and plastic blocks. *Po*2 and *Po*3 were kept in a second terrarium under the same conditions, but with six other conspecifics including males and females. In both of the cases, the artificial light : dark periods were irregularly distributed throughout

Figure 1.—Drawing of an egg of *Promitobates ornatus* after the covering was completed, showing soil particles (black spots) and a fragment of root (arrow) attached to it.

the day. The harvestmen were fed once a week with dead arthropods such as isopods, mosquitoes, drosophilids, pieces of *Tenebrio obscurus* larvae and a variety of plant items (papaya, sugar beet, boiled carrots, beans and rice) and industrial food (cream cheese, cooked ground beef, and bread). They accepted all the items mentioned. All observations were conducted between August 1999 and December 1999.

Females of *P. ornatus* laid isolated eggs over soil surfaces. During oviposition, the female *P. ornatus* stood at legs III and IV, with legs I and II extended forward. The ovipositor extended forward to the genital operculum, at 20° below the horizontal body axis, and the egg slid slowly along it, until the distal part of the ovipositor was reached. At this moment, the female bent the ovipositor bringing it close to the substrate and deposited the egg. Only one egg was laid in each event. In the two cases in which I observed nearly the entire act of oviposition, the times spent for one egg to be laid were 3.4 and 3.5 min. The mean egg length was 1.29 ± 0.16 mm ($n = 8$, range $= 1.05–1.40$ mm), approximately 25% of the female body length (5.10, 5.15, and 5.20 mm). Females laid eggs in the morning ($n = 5$; one not included in Table 1), afternoon ($n = 3$) and at night ($n = 2$), and so apparently did not favor a particular time of day for oviposition.

The time spent by *P. ornatus* to lay one egg was similar to that in other laniatorean species—e.g., 4–12 min for *Pachylus quinamav-*

idensis (Juberthie & Muñoz-Cuevas 1971). The general egg-laying behavior was also similar among the species studied so far, and follows the general description of Juberthie & Muñoz-Cuevas (1971). However, after laying an egg, *P. ornatus* waved legs I over the egg occasionally touching it. Thereafter, the female started scraping the substrate next to the egg with alternate movements of legs I, picking up debris. She then raised legs I and strongly pressed them simultaneously or one at a time against the egg, leaving earth particles attached to it. While scraping, some bigger particles were occasionally brought near the egg, without adhering to it. After she scraped the substrate from one area, she rotated around the egg, stopped turning, and restarted the collection of soil particles from another site. The female's rotation was either clockwise or counterclockwise, with no apparent rule concerning direction or angle of rotation. Alternation of scraping and changing body position was repeated twice or more until the egg covering was complete (Table 1). The mean time spent during egg covering was 37 ± 11 min ($n = 9$, range $= 20–50$ min). Occasionally, between two events of scraping, the female would pass her legs I between the chelae of her chelicerae. This explains why the total time is greater than the sum of partial time periods in Table 1. Before leaving the site, the female tapped the substrate around the egg with the first pair of legs. In one case, 2.3 h elapsed between covering one egg and laying the next one.

Promitobates ornatus apparently does not always choose an appropriate site for collection of soil particles. Female *Po*1 twice laid an egg in sites where she was unable to turn herself around the egg, although she tried to, because the egg was laid too close to a vertical substrate. In addition, females *Po*1 and *Po*2 were observed scraping stones instead of earth surfaces, using the same behavioral patterns described earlier. Thus, the quality of the substrate used for collection of soil particles is probably not the factor that determines the time spent in egg covering. It should be noted, however, that the females always laid their eggs on soil, indicating that they probably recognized and selected soil surfaces for oviposition.

Females of *P. ornatus* did not abort egg laying and egg covering when disturbed by light

Table 1.—Change of body position during nine covering events by three females of *Promitobates ornatus* (*Po*1, *Po*2, and *Po*3). The second column represents the positions adopted by the female. In all cases, 0° is horizontally at left and the angles of rotation have to be counted clockwise. Partial time periods follow the sequence of the location of the female relative to the egg. The lines are organized by animal and hour.

Female	Location of female relative to egg	Partial time periods (min)	Total time (min)	Hour when egg covering started
*Po*1	0°/225°/0°/60°/0°/110°/180°	4/11/4/1/4/9/2	36	0830
*Po*1	0°/225°/180°/270°	13/9/6/5	34	0919
*Po*1	0°/225°/0°/65°/135°	9/10/7/10/5	45	1058
*Po*1	0°/270°/45°/135°	7/12/6/19	45	1135
*Po*1	0°/90°/135°	12/6/5	24	1500
*Po*1	0°/90°/225°	6/7/6	20	0010
*Po*2	0°/180°/340°	24/10/16	51	1836
*Po*3	0°/270°/180°/90°	15/10/4/19	49	1515
*Po*3	0°/45°/290°	10/11/7	29	1950

(*n* = 5) or by the approach of other harvestmen of approximately the same body size [a conspecific male (*n* = 1) and *Ilhaia cuspidata* Roewer 1913 male introduced in the terrarium (*n* = 1)]. On one occasion, a female stopped egg covering and remained motionless when touched on the dorsum with a thin paintbrush. In this case, she waved her second pair of legs searching for the stimulus. Fleeing only occurred when she touched the paintbrush with her second pair of legs.

This reluctance to abandon the eggs has been described in two other Gonyleptidae. Light did not cause females of *Goniosoma proximum* (Mello-Leitão 1922) with eggs to flee (Ramires & Giaretta 1994) and females of *Acanthopachylus aculeatus* (Kirby 1819) guarding eggs fled only under very intense light (Capocasale & Bruno-Trezza 1964). However, in contrast with the behavior displayed by *P. ornatus*, females of *Pachylus quinamavidensis*, while laying an egg, reacted to approaching conspecific males springing with the palps extended towards the male (Juberthie & Muñoz-Cuevas 1971).

No droplets of exocrine gland secretion were noticed on *P. ornatus*' body while laying or covering an egg, but it could be that secretions are added to the legs as they are passed between the chelicerae. Clawson (1988) noted females of two species of Palpatores would rub the exocrine gland openings over their oviposition sites, and suggested this behavior was to mark the sites.

An average of 30 ± 4.97 days (*n* = 5; range = 23–36) of embryonic development was necessary for nymphs of *P. ornatus* to hatch,

less than the 30–60 days found for *Goniosoma spelaeum* (Mello-Leitão 1933) (Gnaspini 1995) and the 45–64 days for *Goniosoma longipes* (Machado & Oliveira 1998). These differences are tentative since temperature greatly influences the duration of embryonic development, and as mentioned above, the laboratory temperature was not controlled during this study. Egg development took 16–27 days for *Cynorta cubana* at 20–28 °C (Juberthie 1972), 13 days at 26 °C and 23–27 days at 20 °C for *Erginulus clavotibialis* (Cambridge 1904) (Goodnight & Goodnight 1976), and 20–38 days for *Vonones sayi* with the temperature ranging from 5–20 °C (Cokendolpher & Jones 1991).

Several invertebrates are known to feed on harvestmen eggs—from conspecifics to flatworms, ants, reduviid bugs, staphylinid beetle larvae, and crickets (Capocasale & Bruno-Trezza 1964; Juberthie & Muñoz-Cuevas 1971; Mora 1990; Gnaspini 1995; Machado & Oliveira 1998). In that context, the energy invested in parental care may be justified because of the resulting (presumed) protection from predation (Alcock 1993). Egg covering in *P. ornatus* lasts an average of 37 min, and the process repeats for each egg laid. Nevertheless, this investment is certainly not as costly as the investments made by females of *Goniosoma spelaeum* and *G. longipes*, which lay clustered eggs and stay with their offspring until the dispersion of the nymphs (sometimes 60–80 days between laying eggs and dispersion) (Gnaspini 1995; Machado & Oliveira 1998).

By laying isolated eggs *P. ornatus* avoids the risk of losing several eggs if an egg happens to be noticed by a predator. Covering eggs with debris is interpreted as a way to hide them from predators (Canals 1936; Juberthie 1972; Cokendolpher & Jones 1991), thus increasing the chances of the embryo's survival. I believe that, in addition to the fact that camouflage makes the eggs difficult to be seen, it may also be effective against predators that use tactile clues. A wandering predator may pass over the egg without noticing it because of the soil particles adhered to the egg. In theory, the greater the number of particles attached and the more uniformly they are distributed on the egg surface, the more effective would be the protection. I believe that there is a strong relationship between the act of changing the body position radially around the egg and the effectiveness of the process. As suggested by Mitchell (1971) for eggs laid in crevices, egg guarding would be of little selective value if the egg is difficult to find.

ACKNOWLEDGMENTS

LITERATURE CITED

Alcock, J. 1993. Animal Behavior: An Evolutionary Approach. 5th ed., Sinauer Associates, Sunderland. 626 p.

Canals, J. 1936. Observaciones biológicas em arácnidos del orden Opiliones. Revista de Chilena de Historia Natural 40:61–63.

Capocasale, R. & L. Bruno-Trezza. 1964. Biologia de *Acanthopachylus aculeatus* (Kirby, 1819) (Opiliones: Pachylinae). Revista de la Sociedad Uruguaya de Entomologia 6:19–32.

Clawson, R.C. 1988. Morphology of defense glands of the opilions (daddylonglegs) *Leiobunum vittatum* and *L. flavum* (Arachnida: Opiliones: Palpatores: Phalangiidae). Journal of Morphology 196:363–381.

Cokendolpher, J.C. & S.R. Jones. 1991. Karyotype and notes on the male reproductive system and natural history of the harvestman *Vonones sayi* (Simon) (Opiliones, Cosmetidae). Proceedings of

the Entomological Society of Washington 93:86–91.

Gnaspini, P. 1995. Reproduction and postembryonic development of *Goniosoma spelaeum*, a cavernicolous harvestman from southeastern Brazil (Arachnida: Opiliones: Gonyleptidae). Invertebrate Reproduction and Development 28:137–151.

Goodnight, M.R. & C.J. Goodnight. 1976. Observations on the systematics, development and habits of *Erginulus clavotibialis* (Opiliones, Cosmetidae). Transactions of the American Microscopical Society 95:654–664.

Juberthie, C. 1965. Données sur l'écologie, le développement et la reproduction des Opilions. Revue d'Ecologie et de Biologie du Sol 2:377–396.

Juberthie, C. 1972. Reproduction et développement d'un opilion Cosmetidae, *Cynorta cubana* (Banks), de Cuba. Annales de Spéléologie 27:773–785.

Juberthie, C. & Muñoz-Cuevas 1971. Sur la ponte de *Pachylus quinamavidensis* (Opilion, Gonyleptidae). Bulletin de la Société d'Histoire Naturelle de Toulouse 107:468–474.

Machado, G. & P.S. Oliveira. 1998. Reproductive biology of the Neotropical harvestman (*Goniosoma longipes*) (Arachnida, Opiliones: Gonyleptidae): Mating, oviposition behaviour, brood mortality, and parental care. Journal of Zoology 246:359–367.

Martens, J. 1993. Further cases of paternal care in Opiliones (Arachnida). Tropical Zoology 6:97–107.

Matthiesen, F.A. 1975. Sobre a postura de *Discocyrtus pectinifemur* Mello-Leitão, 1937 (Opiliones, Gonyleptidae). Ciência e Cultura (São Paulo) 27 suppl:372.

Mitchell, R.W. 1971. Egg and young guarding by a Mexican cave-dwelling harvestman, *Hoplobunus boneti* (Arachnida). Southwestern Naturalist 15:392–394.

Mora, G. 1990. Paternal care in a Neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: Gonyleptidae). Animal Behaviour 39:582–593.

Pinto-da-Rocha, R. 1993. Invertebrados cavernícolas da porção meridional da Província Espeleológica do Vale do Ribeira, sul do Brasil. Revista Brasiliera de Zoologia 10:229–255.

Ramires, E.N. & A.A. Giaretta. 1994. Maternal care in a Neotropical harvestman, *Acutisoma proximum* (Opiliones, Gonyleptidae). Journal of Arachnology 22:179–180.

Rodriguez, C.A. & S. Guerrero. 1976. La historia natural y el comportamiento de *Zygopachylus albomarginis* (Chamberlin) (Arachnida: Opiliones: Gonyleptidae). Biotropica 8:242–247.

COMPARISON OF THE SURVIVAL OF THREE SPECIES OF SAC SPIDERS ON NATURAL AND ARTIFICIAL DIETS

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ABSTRACT. Three species of sac spiders were reared under laboratory conditions to investigate their survival and development. First, the effects of three artificial diets, milk + egg yolk, soybean liquid, and a combination of them, on the survival and development of *Hibana velox* were evaluated. Results over a 10 wk rearing period showed that the percentages of survival of *H. velox* reared on soybean liquid and combination diets did not differ significantly. However, the survival of *H. velox* on the milk + egg yolk diet was significantly lower than on the other two artificial diets. More molts and instars occurred in spiders raised on milk + egg yolk and on the combination diet than on the soybean liquid diet. Second, the development and percent survival of three sac spiders (*Chiracanthium inclusum*, *H. velox*, and *Trachelas volutus*) on artificial diet (i.e., the combination diet) and natural diets (i.e., citrus leafminer larvae and *Drosophila* adults) were compared. The three sac spiders developed into the adult stage on the combination diet. Similarly, all three sac spiders reared on *Drosophila* adults were able to develop to the adult stage. *Chiracanthium inclusum* and *T. volutus* reared on citrus leafminer larvae developed to the adult stage, whereas *H. velox* did not. Females of these three species that matured using combination diet and were fertilized in captivity produced 1–3 egg masses. Oviposition took place 2–7 days after mating. *Chiracanthium inclusum* had an average of 57 eggs per egg mass, whereas *H. velox* and *T. volutus* had an average of 110 and 56 eggs per egg mass, respectively.

Keywords: Laboratory rearing, sac spiders, *Chiracanthium inclusum*, *Hibana velox*, *Trachelas volutus*, citrus leafminer

The diversity of spiders in almost all agroecosystems suggests their importance as predators of insect and other arthropod pests (Whitcomb et al. 1963; Yeargan & Dondale 1974; Carroll 1980; Mansour et al. 1982; Mansour & Whitcomb 1986; Riechert & Bishop 1990; Barrion & Litsinger 1995). Baseline information on life history and biology is fundamental for ecological work and also important to further investigate the potential of spiders as biological control agents. However, life history studies have been done on very few species of spiders. One reason is the lack of reliable rearing methods to determine life histories and other biological data directly from laboratory cultures (Peck & Whitcomb 1968; Whitcomb 1967). Another reason is the lack of appropriate artificial diets. Since spiders are primarily carnivorous, they require behavioral cues from the prey to initiate attack and feeding. This makes the rearing and maintenance of spiders in the laboratory very laborious. Moreover, it appears that most spiders must feed on a variety of insect prey species to obtain the optimum nutrition for survival and reproduction (Greenstone 1979; Uetz et al. 1992). The need to rear different insect prey species makes it especially difficult to culture spiders in the laboratory. Formulation of artificial diets would greatly facilitate laboratory rearing of spiders; however, knowledge of the nutritional requirements for spiders is necessary.

It was reported that some species of wan-

dering spiders are facultative nectar feeders (Taylor & Foster 1996). This finding inspired us to compare the survival of spiders on different artificial diets. Preliminary results of our previous study on the survival of the sac spider *Hibana velox* (Becker 1879) showed that spiders reared on soybean diet had a higher survival rate but slower rate of development than spiders reared on milk + egg yolk or on sugar solution alone (Amalin et al. 1999). This present study is a follow up of our previous experiment on the survival of *H. velox* raised on different artificial diets. We investigated the effect of different artificial diets including the previously tested (milk + egg yolk and soybean liquid) diets and a new diet (combination diet) on the survival and development of *H. velox*. The nutritional composition of each diet is evaluated in relation to the survival and development of the spider. Also, the various degrees of survival of the three species of sac spiders, *Chiracanthium inclusum* (Hentz 1847), *H. velox*, and *Trachelas volutus* Gertsch 1935 are compared when they were reared on artificial and natural diets. These sac spiders actively hunt their prey at night and during the day they hide in tubular silken capsules that they construct (hence the name "sac spiders"). For this study, the three species of sac spiders mentioned above were selected as the test organisms because they were found associated with citrus leafminer, which is one of the major insect pests of lime in south Florida (Amalin 1999).

METHODS

Comparison of artificial diets.—The three different artificial diets evaluated with respect to the survival of *H. velox* were soybean liquid (non-dairy beverage, Edensoy™ Eden Foods Inc.), milk + egg yolk mixture (100 ml homogenized whole milk + 1 fresh chicken egg yolk), and their combination(1:1 soybean and milk + egg yolk mixture). One ml of green food color (McCormick™) was added to each diet to serve as an indicator of whether the spiders fed on the liquid diet since the color of their abdomen changes depending on the color of the food they consumed. The nutritional composition for each diet is shown in Table 1. A single first instar spiderling of *H. velox* was placed in a glass vial (15 mm diameter × 60 mm long) (Fig. 1A). The mouth of the vial was closed with a cotton swab sat-
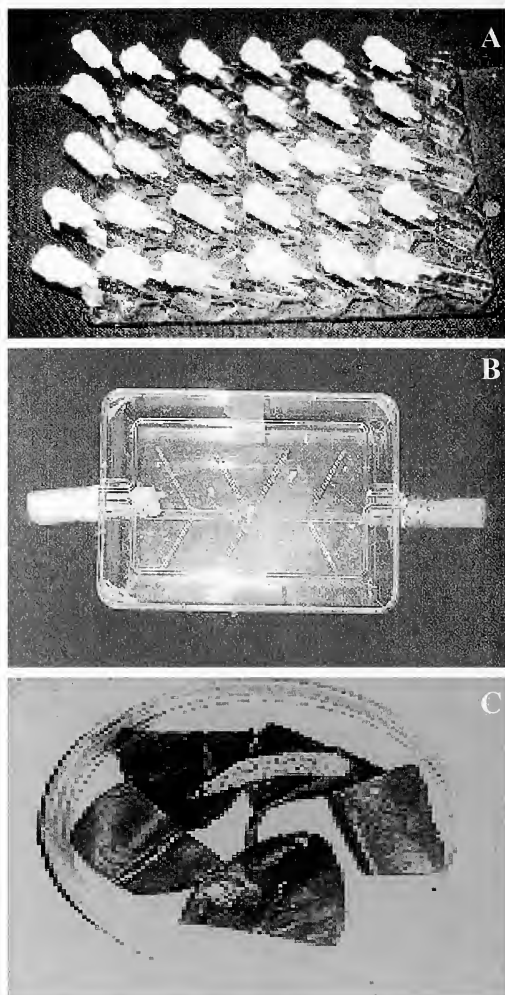

Figure 1.—Set-up for rearing spiders. (A). On the combination diet. (B). On adults of *Drosophila*. (C). On larvae of the citrus leafminer.

urated with the liquid diet. A one-inch long stick was impaled in the swab with the end pointing to the interior of the vial. The spider perched on the stick as it fed on the diet. The diet was replaced with fresh ingredients on a cotton swab every two days. The treatments for each artificial diet were replicated three times with 20 spiderlings per replication. All vials were kept in an incubator at 27 °C, 80% RH and a L:D 12:12 photoperiod. Spider mortality and molting were recorded every two days for 10 wk. The rate of development and growth in the different artificial diets was compared using one-way analysis of variance (ANOVA) (SAS institute 1989).

Nature/sources of artificial and natural

Table 1.—Nutritional composition of the different diets based on the manufacturers' nutritional analyses per 100 ml.

Nutrient composition	Milk + egg yolk	Soybean	Combination diet
Total fat	3.04 g	1.30 g	4.34 g
Saturated fat	1.30 g	0.0 g	1.3 g
Cholesterol	97.83 mg	0.0 mg	97.83 mg
Sodium	82.61 mg	39.13 mg	121.74 mg
Total carbohydrates	6.09 g	10.87 g	17.04 g
Sugars	5.22 g	6.52 g	12.99 g
Protein	6.04 g	2.61 g	8.65 g
Potassium	0.0 mg	126.09 mg	126.09 mg
Vitamin A	348.00 IU	0.0 IU	348 IU
Thiamin (B1)	0.0 mg	0.05 mg	0.05 mg
Riboflavin (B2)	0.0 mg	0.03 mg	0.03 mg
Niacin (B3)	0.0 mg	0.52 mg	0.52 mg
Pantothenic acid (B5)	0.0 mg	0.35 mg	0.35 mg
Pyridoxine hydrochloride (B6)	0.0 mg	0.05 mg	0.05 mg
Folate (B9)	0.0 mg	0.02 mg	0.02 mg
Vitamin C	0.52 mg	0.0 mg	0.52 mg
Vitamin D	43.48 IU	0.0 IU	43.48 IU
Biotin (Vitamin H)	0.0	0.0003 g	0.003 g
Calcium	0.14 g	0.03 g	0.17 g
Iron	0.31 mg	0.31 mg	0.62 mg
Phosphorus	0.11 g	0.04 g	0.15 g
Magnesium	0.0 mg	17.4 mg	17.4 mg
Zinc	0.0 mg	0.26 mg	0.26 mg

diets.—The composition of the artificial diet for rearing of spider colonies was similar to the combination diet (Table 1) to which 5 ml honey was added. The natural diets consisted of either adults of the fruit fly, *Drosophila melanogaster* Meigen 1830, or larvae of the cit-rus leafminer, *Phyllocnistis citrella* Stainton 1856. The fruit flies were mass reared in the laboratory at 25–27 °C and 70–80% RH. The initial population of fruit flies was obtained by exposing over-ripe bananas in a glass jar. The

Table 2.—Percentages of survival of *Hibana velox* during 10 weeks on three different artificial diets under laboratory conditions at 27° C and 80% RH. Means followed by the same letters in the same row are not significantly different ($P \leq 0.05$) according to Duncan's Multiple Range Test.

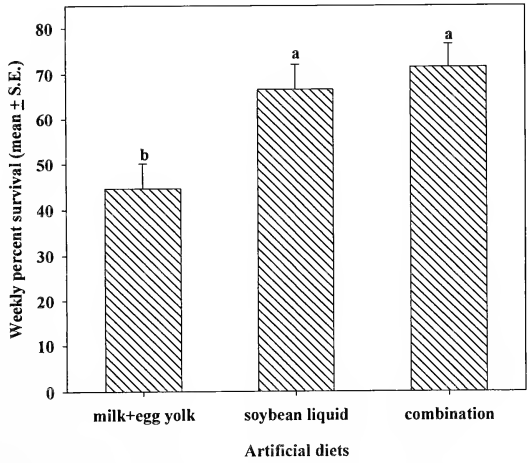|	Artificial diets		
Week	Milk + yolk	Soybean	Combination
1	86.67 a	95.53 a	95.57 a
2	86.63 a	95.53 a	95.57 a
3	68.87 b	93.30 a	95.57 a
4	60.00 b	86.70 a	88.87 a
5	46.67 b	77.77 a	86.67 a
6	39.97 b	73.33 a	66.67 a
7	26.67 bc	53.33 ab	57.77 a
8	22.33 b	51.10 a	51.10 a
9	17.80 b	42.20 a	42.23 a
10	17.80 b	42.20 a	42.23 a

Figure 2.—Mean weekly survival of *Hibana velox* reared on different artificial diets. Bars with the same letters are not significantly different according to Duncan's Multiple Range Test ($P \leq 0.05$).
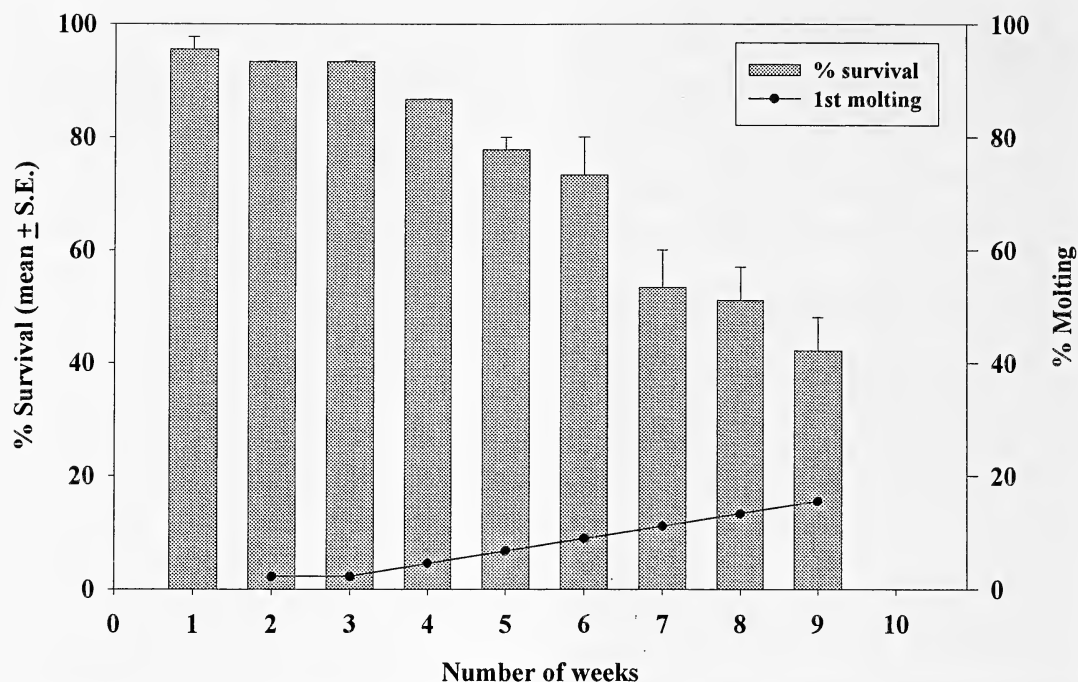
Figure 3.—Weekly percentages of survival and molting of *Hibana velox* reared on soybean liquid diet.

fruit fly adults trapped in the jar were reared using the banana medium described by Yoon (1985), with some modifications. Approximately 10 ml of the medium were poured from a sterilized beaker into each sterilized glass vial (15 mm diameter × 60 mm long). After the medium cooled, a sterilized strip of filter paper (1 cm × 5 cm) was inserted into each vial. The mouth of the vial was plugged with a sterilized cotton ball. The vials were stored for a day at 20 °C before use or stored at 4 °C until needed. Adult fruit flies from the initial population were immobilized by placing them in a freezer (~0 °C) for 30–40 s and transferred to an empty glass jar. Ether was used for a longer period of immobilization. Next, five males and five females were transferred to each glass vial containing banana medium. The fruit fly cultures were kept in an incubator at 27 °C and 80% RH. Adults from the succeeding cultures were mass reared. To avoid inbreeding, adult fruit flies from different stock cultures were mixed for re-culturing. A 1 wk-old fruit fly culture was utilized for spider rearing. This provided a continous supply for the spider in the rearing cage for 3–4 wk.

Citrus leafminer larvae were collected from

an unsprayed lime orchard or from a greenhouse culture on lime shoots.

Test spiders.—Egg sacs of *C. inclusum, H. velox* and *T. volutus* were collected in the field, brought to the laboratory and maintained in an incubator at 27 °C and 80% RH until spiderling emergence. Egg sacs were identified based on the description by Amalin et al. (1999). First instar spiderlings were used in the experiment. Voucher specimens are deposited at the Tropical Research and Education Center (TREC), Entomology Division at Homestead, Florida.

Experimental protocol.—Three different containers were used for artificial and natural rearing. These rearing containers were used based on the preliminary trial we conducted on different rearing containers for each diet. They were selected for ease of handling of the spiders with minimal injury and disturbance, and also for speed in replacing the diet. The cage size might have an effect on the feeding behavior of the spiders, but this was not considered in this study. The spiders fed with artificial diet were placed in glass vials (15 mm diameter × 60 mm long) (Fig. 1A) as explained in the experiment on the comparison of artificial diets. To rear the spiders on *D.*
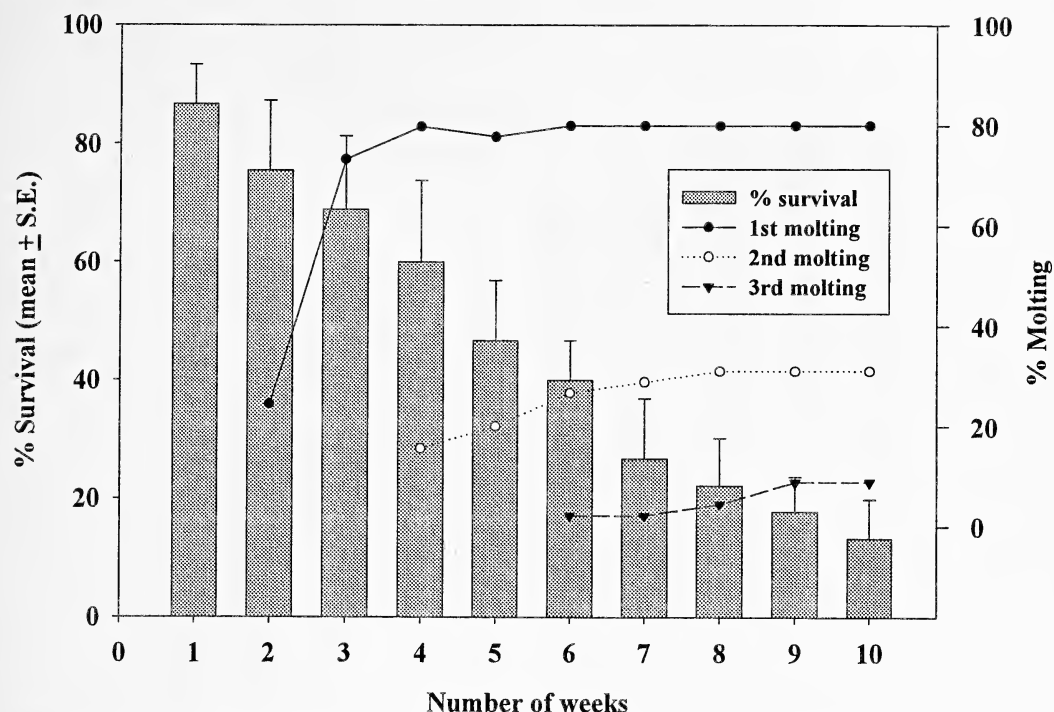
Figure 4.—Weekly percentages of survival and molting of *Hibana velox* reared on milk + yolk diet.

melanogaster, newly emerged spiderlings were placed individually in a translucent plastic box (70 cm high × 70 cm long × 20 cm wide) (Fig. 1B) with two circular openings (2 cm diameter) in the opposite sides. A 30 ml vial containing 10 ml of water was plugged with cotton and inserted into the one opening of the box. A glass vial containing a 1 wk-old culture of *D. melanogaster* adults on banana medium was introduced through the second circular opening. The spiders fed with 10 second instar *P. citrella* larvae were placed with these prey inside a plastic petri dish (10 cm in diameter × 1 cm high) lined with moistened filter paper (Fig. 1C).

Thirty spiders of each species were reared from egg to maturity on the different diets. All spiders were maintained in an incubator at 27 °C and 80% RH with a L:D 12:12 photoperiod. The artificial diet and *P. citrella* larvae were replaced every 2 days, whereas *D. melanogaster* cultures were checked every 2 wk and replaced as needed. The survival and the developmental rates of the three sac spiders reared on artificial and natural diets were compared using Duncan Multiple Range Test (SAS Institute 1989).

RESULTS

Comparison of artificial diets.—Spiders raised on milk + egg yolk diet had a significantly lower weekly percentage survival than those reared on soybean liquid diet and the combination diet (Fig. 2). Table 2 shows the percentage spider survival weekly for a period of 10 wk. During wk 1 and 2, percentages of spider survival did not differ significantly among the three artificial diets. From wk 3 to wk 10, the percentages of spider survival were significantly higher for soybean liquid and combination diets than the milk + egg yolk mixture diet. In wk 7, percentages of spider survival on soybean liquid did not differ significantly from that of milk + egg yolk and combination diets. However, percentage survival was significantly higher on combination diet than on milk + egg yolk diet.

The developmental growth of *H. velox* reared on the different artificial diets was recorded based on weekly survival and percentages of molting (Figs. 3–5). The growth of spiders differed on the various artificial diets. Only 2% of the spiders raised on soybean liquid diet underwent one single molt during
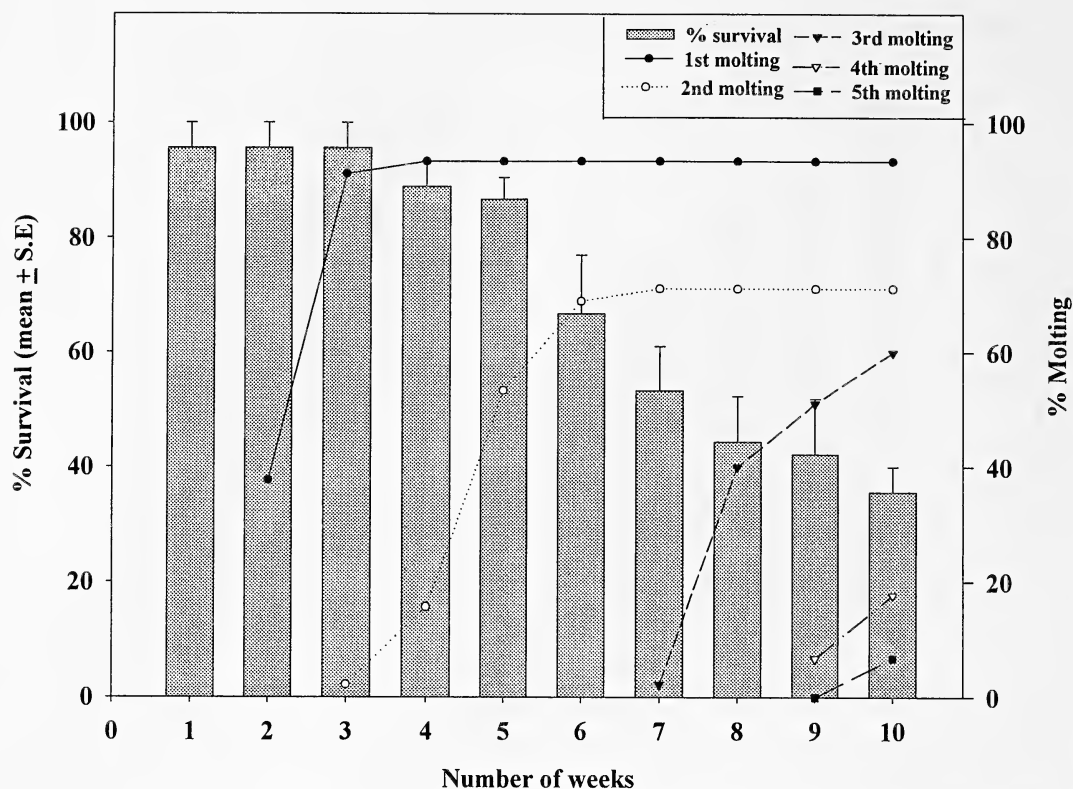
Figure 5.—Weekly percentages of survival and molting of *Hibana velox* reared on combination diet.

the second and third weeks of rearing (Fig. 3). The peak of molting was observed during week 9. Percentage survival of *H. velox* on soybean liquid diet was relatively high. More than 90% survived from week 1 to week 3 and 80% from from week 4 to week 6. During weeks 7 to 9, percentage survival decreased to less than 50% and by week 10 all of the spiders raised on this diet died (Fig. 3).

Spiders reared on milk + egg yolk mixture and combination diets underwent more molts than those reared on soybean liquid diet (Figs. 4, 5). Spiders raised on milk + egg yolk diet molted three times (Fig. 4). A mean of 34.4% of the total spiders molted in week 2 and the percent that molted increased as the rearing progressed. The frequency of first molts peaked in week 4 and remained level. Eighty percent of the surviving spiders molted at least once. Almost 50% of the surviving spiders underwent a second molt between weeks 4 and 10, third molts started on week 6 until week 10. Percentage survival drastically decreased from week 1 to week 10, from 85% to 9%. Spiders raised on the combination diet

underwent as many as five molts (Fig. 5). First molts started during week 2, with a mean of almost 40%, and reached 93.3% by week 4. Second molts started during week 3, which was a week earlier than on milk + egg yolk diet; however, the percentage of second molts rose during week 4 and peaked in week 6. Third molts peaked during week 10. However, very few spiders reared on combination diet underwent the fourth and fifth molts. The trend of the percentage survival of spiders reared on the combination diet was similar to that on the soybean liquid diet except on week 10 in which almost 40% were still surviving.

Comparison of artificial and natural diets.—The developmental stages and percentages of survival for each developmental stages of the three sac spider species reared on artificial and natural diets are shown in Figs. 6–8. On the combination diet, all three species were able to develop into the adult stage (Fig. 6), after the sixth and seventh molts. In general, percentages of survival of *H. velox* were relatively higher than those of *C. inclusum* and *T. volutus* in all developmental stages on
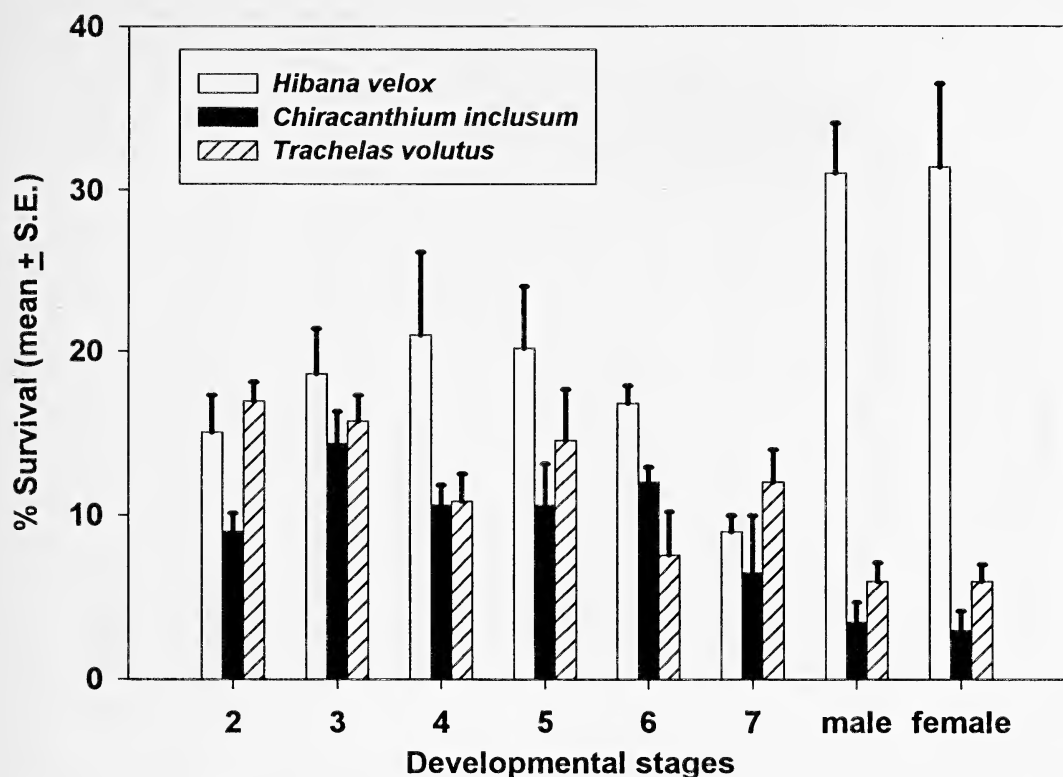
Figure 6.—Survival of developmental stages of *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus* reared on combination diet.

the combination diet. Moreover, percentage survival to adulthood was higher for *H. velox* than for *C. inclusum* and *T. volutus*. From the surviving spiders in the sixth and seventh molt stages, 31% and 32% of *H. velox* developed into male and female adults, respectively. Survival was less than 10% for *C. inclusum* and *T. volutus*. Females that matured on combination diet and were fertilized in captivity produced one to three egg masses. Oviposition took place 2–7 days after mating for all three species. The number of eggs laid by female *H. velox* ranges from 96–120 with an average of 110. The number of eggs per egg mass of *C. inclusum* reared in the laboratory varied from 36–86 with an average of 57. Edwards (1958) reported 112 eggs in a single egg mass and Peck & Whitcomb (1970) reported a range of 17–86 eggs per egg mass. *Trachelas volutus* produced 47–66 per egg mass with an average of 56.

The three species of sac spiders reared on *Drosophila* were able to develop into the adult stage (Fig. 7). In general, percentage survival of *T. volutus* was relatively higher than those of *H. velox* and *C. inclusum* for the immature stages. However, *C. inclusum* and *H. velox* had higher percentages survival to the adult stage. Less than 10% from the seventh and eighth molt stages survived into male and female adults for *T. volutus*. For *C. inclusum*, 30% and 38% from the seventh and eighth molt stages developed into male and female adults, respectively. For *H. velox*, 17% developed into male and 12% into female adults.

In general, percentage survival of *T. volutus* was relatively higher than those of *H. velox* and *C. inclusum* when reared on *P. citrella*. *Trachelas volutus* and *C. inclusum* successfully developed into the adult stage but *H. velox* did not (Fig. 8). This finding suggests that *P. citrella* is deficient in one or more nutrients required by *H. velox*. However, the consumption of *P. citrella* by immature *H. velox* was relatively higher than by *C. inclusum* and *T. volutus*.
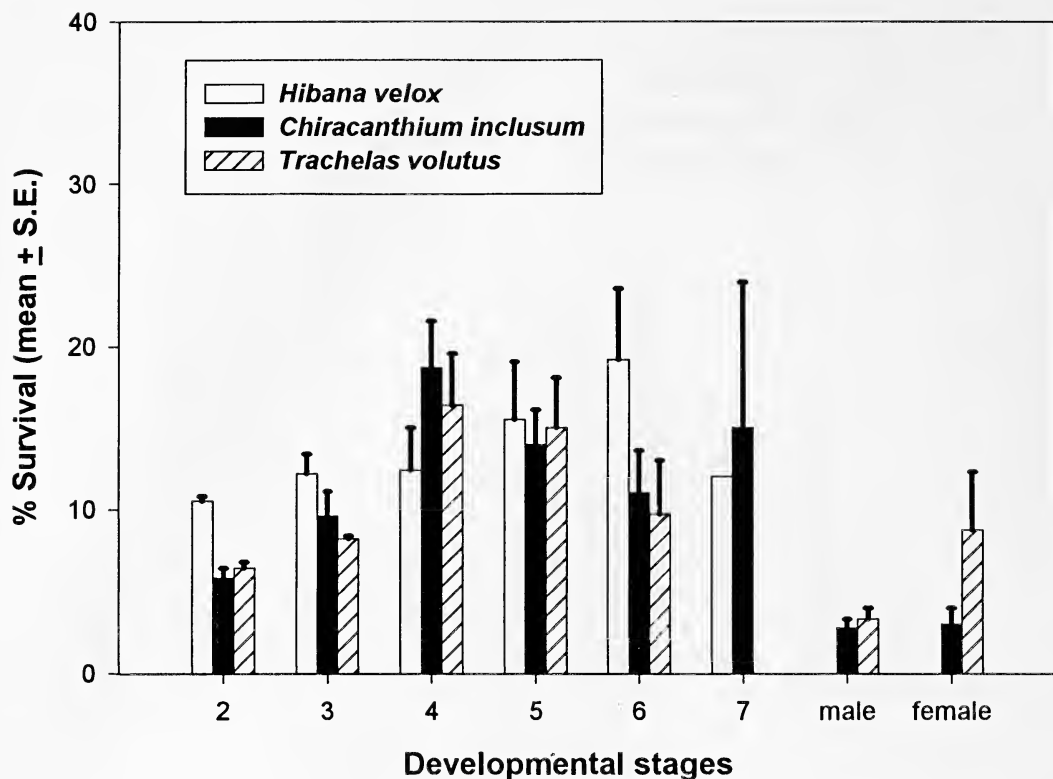
Figure 7.—Survival of developmental stages of *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus* reared on adults of *Drosophila*.

DISCUSSION

Each single diet has an important nutrient for the growth and survival of spiders under laboratory conditions. For instance, on soybean liquid and combination diets the following nutrients are available in relatively higher amounts: carbohydrates, sugar, potassium, magnesium, and zinc. Among these nutrients, carbohydrates are known to be the major energy source important for survival or longevity of any arthropod species, whereas the minerals potassium, magnesium, and zinc are necessary for optimal growth (Singh 1984). Vitamin B-complex is also required in artificial diets and is available in soybean liquid but absent in milk + egg yolk diet. This finding suggests that if enough carbohydrates, and possibly the other nutrients mentioned above are available, mortality at an early stage of spider development will be avoided. However, results from our previous experiment (Amalin et al. 1999) revealed that the development of spiders on soybean liquid was delayed but progressed normally on milk + egg yolk diet.

The main nutrient that is available in milk + egg yolk diet, which is absent in soybean liquid, is cholesterol. Cholesterol is a common sterol and a precursor of ecdysone, the molting hormone (Foelix 1982; Singh 1984). This may explain the delayed development of spiders on soybean diet. Other nutrients available in relatively higher amounts in milk + egg yolk diet are total fat, saturated fat, sodium, protein, Vitamin A, Vitamin D, calcium, and phosphorous. These nutrients may also contribute to the complete development of spiders on milk + egg yolk diet. According to House (1961) an artificial diet should contain a balance of proteins, carbohydrates, lipids, and vitamins for normal growth, development, reproduction and other life processes. All of these important nutrients are available in the combination diet with more concentrated values (Table 1), which probably explains the higher percent survival and normal development of spiders on the combination diet than on the soybean and milk + egg yolk diets. The completion of development of the three
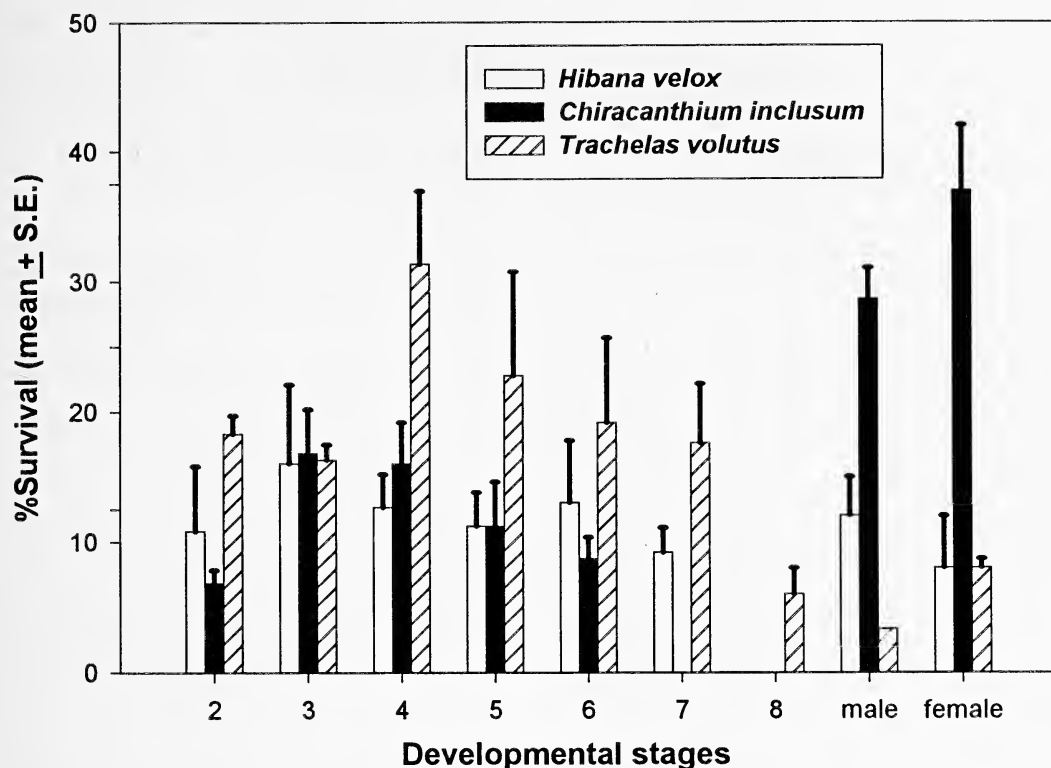
Figure 8.—Survival of developmental stages of *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus* reared on larvae of citrus leafminer.

species of sac spiders on the combination diet suggests that they are also nectar feeders as reported by Taylor & Foster (1996). This further suggests that the combination diet provided more complete nutrional or dietary requirements for sac spiders. Nevertheless, different species of spiders even under the same guild or group could have different requirements of the proportion of all the nutrients pertinent to survival and development. This might be one reason why there was a higher percentage survival of *H. velox* fed with combination diet than *C. inclusum* and *T. volutus*. Thus, we recommend that different proportions of the nutrients of the combination diet should be tried to determine the best proportion of each one for the survival and development of these three species of sac spiders. Behavioral and ecological differences among these three species of sac spiders should not be ruled out as possible reasons for differences in percentage survival; however, any such differences were not observed in this particular study. Of the natural diets tested,

Drosophila provided a suitable diet for the three species of spiders particularly for *H. velox* and *C. inclusum*; whereas, citrus leafminer seems to be less suitable as diet of the spiders under laboratory conditions.

Results from this experiment reveal that an artificial diet is adequate for these spiders under laboratory conditions. Attempts towards the mass rearing of these spiders using artificial diets should be pursued. Clearly the proportions of the various ingredients in combination diet must be evaluated to optimize spider survival and reproduction. Advancements in mass-rearing spiders on artificial diets may enable their use in agriculture for augmentation of field populations.

ACKNOWLEDGMENTS

LITERATURE CITED

Amalin, D.M. 1999. Evaluation of Predatory Spiders as Biological Control Agents of Citrus Leafminer, *Phyllocnistis citrella*, in Lime Orchards at Homestead, Florida. Ph.D. dissertation, University of Florida, Gainesville.

Amalin, D.M., J. Reiskind, R. McSorley & J. Peña. 1999. Survival of the hunting spider, *Hibana velox* (Arneae, Anyphaenidae), raised on different artificial diets. Journal of Arachnology 27(2): 692–696.

Barrion, A.T. & J.A. Litsinger. 1995. Riceland Spiders of South and Southeast Asia. Centre for Agriculture and Biosciences International, Wallingford, Oxon, England. 700 pp.

Carroll, D.P. 1980. Biological notes on the spiders of some citrus groves in central and southern California. Entomological News 91:147–154.

Edwards, R.J. 1958. The spider subfamily Clubioninae of the United States, Canada, and Alaska (Araneae: Clubionidae). Bulletin of the Museum of Comparative Zoology 118:365–434.

Foelix, R. 1982. Biology of Spiders. Harvard Univ. Press, Cambridge, Massachusetts. 306 pp.

Greenstone, M.H. 1979. Spider feeding behaviour optimises dietary essential amino acid composition. Nature 282:501–503.

House, H.L. 1961. Insect nutrition. Annual Review of Entomology 6:13–26.

Mansour, F. & W.H. Whitcomb. 1986. The spiders of a citrus grove in Israel and their role as biocontrol agents of *Ceroplastes floridensis* (Homoptera: Coccidae). Entomophaga, 31:269–276.

Mansour, F., J.W. Ross, G.B. Edwards, W.H. Whitcomb & D.B. Richman. 1982. Spiders of Florida citrus groves. Florida Entomologist 65:514–522.

Peck, W.B. & W.H. Whitcomb. 1968. Feeding spiders on artificial diet. Entomological News 79: 233–236.

Peck, W.B. & W.H. Whitcomb. 1970. Studies on the biology of a spider, *Chiracanthium inclusum* (Hentz). Florida Agricultural Extension Station Bulletin 753:1–76.

Riechert, S.E. & L. Bishop. 1990. Prey control by an assemblage of generalist predators in a garden test system. Ecology 71:726–736.

SAS Institute. 1989. SAS/STAT User's Guide, version 6, 3rd ed., Vol. 2. SAS Institute Inc., Cary, North Carolina, 846 pp.

Singh, P. 1984. Insect diets. Historical developments, recent advances, and future prospects. Pp. 32–44. *In* Advances and Challenges in Insect Rearing. (E.G. King & N.C. Leppla, eds.). Agricultural Research Service, Southern Region, U.S. Department of Agriculture, New Orleans, 306 pp.

Taylor, R.M. & W.A. Foster. 1996. Spider nectarivory. American Entomologist 82–86.

Uetz, G.W., J. Bischoff & J. Rovner. 1992. Survivorship of wolf spiders (Lycosidae) reared on different diets. Journal of Arachnology 20:207–221.

Whitcomb, W.H. 1967. Wolf and lynx spider life histories. *In* Terminal Report to National Science Foundation. Univ. of Arkansas. Div. of Agriculture, Dept. of Entomology. Fayetteville, Arkansas. 142 pp.

Whitcomb, W.H., H. Exline & R.C. Hunter. 1963. Spiders of the Arkansas cotton field. Annals of the Entomological Society of America 56:653–660.

Yeargan, K.V. & C.D. Dondale. 1974. The spider fauna of alfalfa fields in northern California. Annals of the Entomological Society of America 67:681–682.

Yoon, J.S. 1985. Drosophilidae: *Drosophila melanogaster*. Pp.75–91. *In* Handbook of Insect Rearing, Vol. II (P. Singh & R.F. Moore, eds.). Elsevier Science Publishing Company, New York, 514 pp.

SHORT COMMUNICATION

POST-MATURATION MOLT FOUND IN A WOLF SPIDER, *PARDOSA ASTRIGERA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. An adult female *Pardosa astrigera* (Araneae, Lycosidae) died failing to finish an additional molt in the laboratory. Its maturity was morphologically ascertained by SEM examination.

Keywords: Lycosidae, *Pardosa astrigera*, post-maturation molt

Post-maturation molt is well known in females of the primitive spiders (Liphistiomorphae and Mygalomorphae) which continue to grow for several years after sexual maturation (Baerg & Peck 1970; Main 1976; Stradling 1978; Stewart & Martin 1982; Yoshikura 1987; Maki 1989; Miyashita 1992). Post-maturation molt, however, is very rare among entelegynes and has been reported only for six females in three species: three in *Latrodectus mactans* (Fabricius 1775) (Theridiidae) (Kaston 1968), two in *L. hesperus* Chamberlin & Ivie 1935 (Kaston 1968), and one in *Heteropoda venatoria* (L. 1758) (Sparassidae) (Kayashima 1981). This report documents one more entelegyne post-maturation molt found in a female wolf spider (Lycosidae), *Pardosa astrigera* L. Koch 1878. This female was captured on 11 June 1983 at Hidaka, in northwestern Kanto Plain, central Japan. It molted to maturity on 30 June, and died on 3 August of that year, after failing to extract its extremities during the additional molt. It was then preserved in 70% ethanol. *Pardosa astrigera* is common on the sunny ground with sparse vegetation (Fujii 1998) and is found also in Korea and China (Tanaka 1993). Its ecophysiological characteristics were heavily studied (Miyashita 1968a, 1968b, 1969a, 1969b, 1998; Fujii 1974, 1978, 1980; Tanaka & Itô 1982), though this spider had been identified with a closely related species, *Pardosa (Lycosa) T-insignita* until the examination by Tanaka (1980).

Sclerification and lengthening of epigyna in females of *Schizocosa ocreata* (Hentz 1844) (Lycosidae) begin by the third or fourth instar prior to maturation (Amaya & Klawinski 1996). Thus, one may sometimes confuse an immature female with a mature one when observing it with a magnifying glass or the naked eye. The females reported by Kaston (1968) and Kayashima (1981) had undoubtedly matured because they copulated and laid fertile eggs before the additional molt. On the other hand, this *P. astrigera* female refused the courtship of a male and killed it. This female left no evidence of egg-cocoon construction, which sometimes occurs even in virgin females. Its maturity was ascertained by the morphological observations described below.

In many lycosid species, knob-tipped hairs (knobbed hairs) peculiar to adult female abdomens were found (Graefe 1964; Rovner et al. 1973). Also in *P. astrigera*, I found the hairs on adult females (Fujii 1983), but not on subadult females nor on males. If the *P. astrigera* female actually had matured before the final molt, a well-developed epigynum (with genital openings) and knobbed hairs should be found on the old (molted) exuvium of its abdomen. The specimen was observed with a digital optical microscope (Keyence VH-Z05) (Fig. 1), then was examined with a scanning electron microscope (Hitachi S-4000) after critical point drying and ion-beam sputter coating with Pt-Pd (Figs. 2–7). A well-developed epigynum was seen in the area of old exuvium (Figs. 1–3), and its external features coincided with those of the standard epigynum illustrated in Tanaka (1980, 1993). Many knobbed hairs were also detected on both old and new exuviae (Figs. 6, 7). From these re-
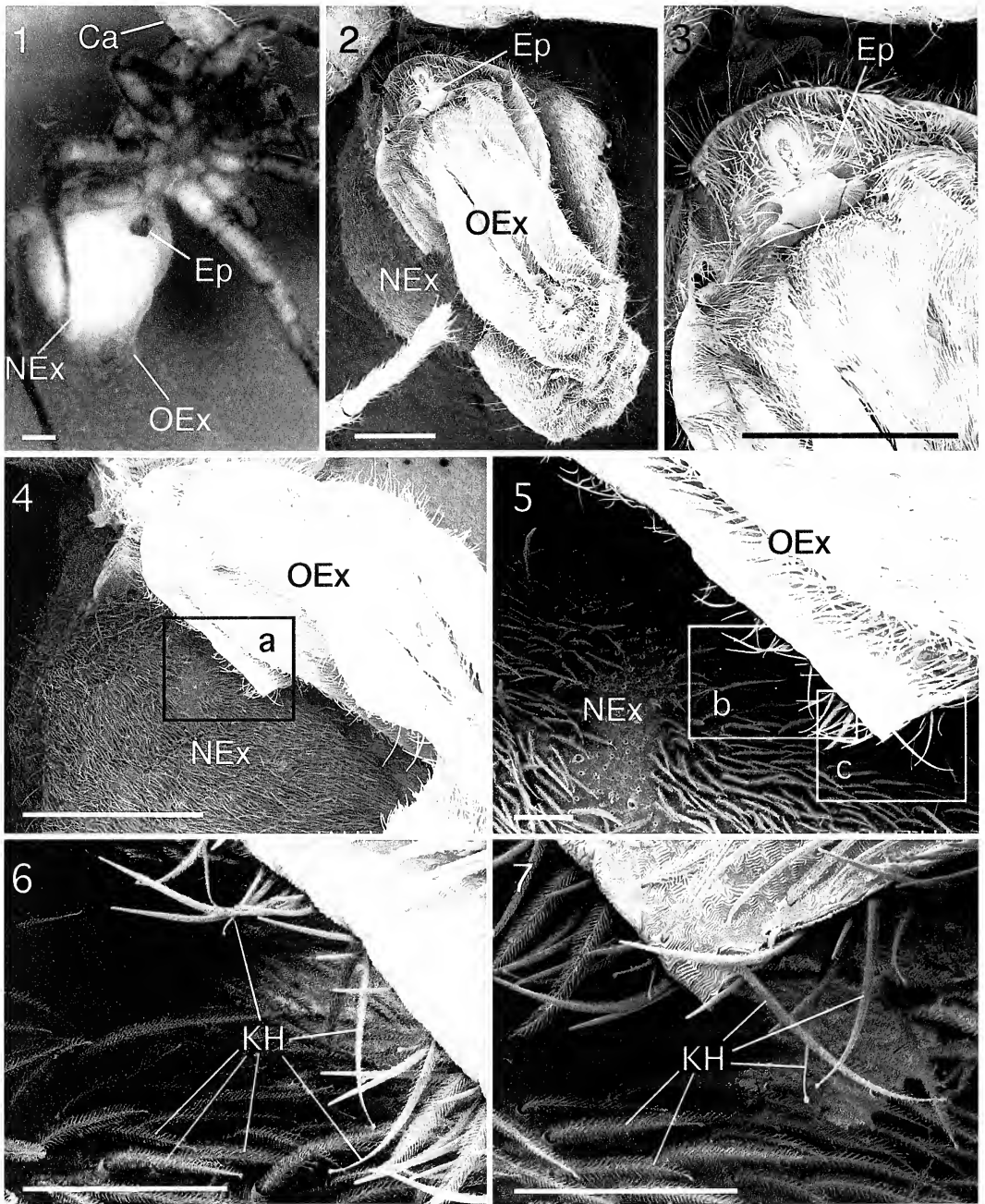
Figures 1–7.—A female of *Pardosa astrigera* that died at an additional molt after maturation. 1. The female in 70% ethanol before treatments for electron microscopic observation; 2–7. Scanning electron micrographs of the ventral side of the abdomen. 2. The whole abdomen; 3. The epigynum on the old exuvium; 4, 5. The old and new exuviae in the mid-dexter portion (5 corresponds to 4a); 6, 7. Knobbed hairs both on the old and new exuviae (6 and 7 correspond to 5b and 5c, respectively). *Abbreviations:* Ca = carapace, Ep = epigynum, KH = knobbed hairs, NEx = new exuvium, OEx = old exuvium. *Scale bars:* Figures 1–4 = 1 mm, Figures 5–7 = 0.1 mm.

sults it can be said that post-maturation molt occurred in this lycosid. Renewal of the epigynum at this molt could not be seen in this specimen as well as in the Kaston's females. This specimen was deposited as the voucher in the collection of the Department of Zoology, National Science Museum, Tokyo (NSMT-Ar 4321).

If the post-maturation molt of entelegynes were part of a reproductive strategy, it would be expected to occur only in extremely old or small females. But the female of *P. astrigera* molted only 34 days after maturation, while females of this species usually live for a longer period (143 days is the longest known). Moreover, its carapace width reached to 3.2 mm at maturity. This size is not small compared to the range of 2.2–3.5 mm in adult females of *P. astrigera* collected in the field (Fujii unpubl. data). This additional molt could not be found in the other 368 females of 18 lycosid species (50 females of *P. astrigera*), which had matured in the field (216 females) or the laboratory (152 females) from 1981–1987 and were reared until the death to examine their life cycles. This molt may be an accidental phenomenon occurring at very low frequency (0.27% for the total lycosids) and seems to occur also in natural lycosid populations.

ACKNOWLEDGMENTS

LITERATURE CITED

Amaya, C.C. & P.D. Klawinski. 1996. A method for assessing gender in immature wolf spiders (Araneae, Lycosidae). Journal of Arachnology 24:158–160.

Baerg, W.J. & W.B. Peck. 1970. A note on the longevity and molt cycle of two tropical theraphosids. Bulletin of the British Arachnological Society 1:107–108.

Fujii, Y. 1974. Hunting behaviour of the wolf spider, *Pardosa T-insignita* (Boes. et Str.). Bulletin of the Nippon Dental College General Education 3:135–148.

Fujii, Y. 1978. Examinations of the maternal care of cocoon in *Pardosa astrigera* L. Koch (Araneae, Lycosidae). Bulletin of the Nippon Dental University General Education 7:221–230.

Fujii, Y. 1980. Analytical study of maternal behaviour in *Pardosa astrigera* L. Koch (Araneae, Lycosidae). Bulletin of the Nippon Dental University General Education 9:233–245.

Fujii, Y. 1983. Four *Arctosa* lycosids lacking the abdominal knobbed hairs and their pulli's post-emergent behaviour (Araneae, Lycosidae). Bulletin of the Nippon Dental University General Education 12:177–188.

Fujii, Y. 1998. Ecological studies on wolf spiders (Araneae: Lycosidae) in a northwest area of Kanto Plain, central Japan: Habitat preference observed by hand-sorting. Acta Arachnologica 47: 7–19.

Graefe, G. 1964. Die Brutfürsorge bei *Pardosa lugubris* (Walckenaer 1802) (Araneae, Lycosidae). Ph.D. thesis, Ludwig-Maximilians-Universität, München.

Kaston, B.J. 1968. Remarks on black widow spiders, with an account of some anomalies. Entomological News 79:113–124.

Kayashima, I. 1981. A report on long-term rearing of *Heteropoda venatoria* (Linné) (1). Kishidaia (47):57–64. (in Japanese)

Main, B.Y. 1976. Spiders. Collins, Sydney.

Maki, T. 1989. Life history of the trapdoor spider *Latouchia typica* (Kishida). Atypus 94:18–25. (in Japanese)

Miyashita, K. 1968a. Growth and development of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae) under different feeding conditions. Applied Entomology and Zoology 3:81–88.

Miyashita, K. 1968b. Quantitative feeding biology of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae). Bulletin of the National Institute of Agricultural Sciences (Japan), Series C 22:329–344.

Miyashita, K. 1969a. Seasonal changes of population density and some characteristics of overwintering nymph of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae). Applied Entomology and Zoology 4:1–8.

Miyashita, K. 1969b. Effects of locomotory activity, temperature and hunger on the respiratory rate of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae). Applied Entomology and Zoology 4: 105–113.

Miyashita, K. 1992. Postembryonic development and life cycle of *Atypus karschi* Dönitz (Araneae: Atypidae). Acta Arachnologica 41:177–186.

Miyashita, K. 1998. Egg sac production and nymphal development of *Pardosa agraria* Tanaka and *Pardosa astrigera* L. Koch under a seminatural condition. Journal of the Natural History Museum and Institute, Chiba 5:41–45. (in Japanese)

Rovner, J.S., G.A. Higashi & R.F. Foelix. 1973. Maternal behavior in wolf spiders: The role of abdominal hairs. Science 182:1153–1155.

Stewart, D.M. & A.W. Martin. 1982. Moulting in the Tarantula, *Dugesiella hentzi*. Journal of Comparative Physiology 149:121–136.

Stradling, D.J. 1978. The growth and maturation of the "tarantula," *Avicularia avicularia* L. Zoological Journal of Linnean Society 62:291–303.

Tanaka, H. 1980. Notes on four type-specimens of Japanese wolf spiders of the Museum für Naturkunde, Humbolt Universität, Berlin. Acta Arachnologica 29:47–55.

Tanaka, H. 1993. Lycosid spiders of Japan XI. The genus *Pardosa* C.L. Koch – *paludicola*-group. Acta Arachnologica 42:159–171.

Tanaka, K. & Y. Itô. 1982. Decrease in respiratory rate in a wolf spider *Pardosa astrigera* (L. Koch), under starvation. Researches on Population Ecology 24:360–374.

Yoshikura, M. 1987. The Biology of Spiders. Japan Scientific Societies Press, Tokyo. (in Japanese)

SHORT COMMUNICATION

DESCRIPTION OF THE EGG SAC OF *MIMETUS NOTIUS* (ARANEAE, MIMETIDAE) AND A CASE OF EGG PREDATION BY *PHALACROTOPHORA EPEIRAE* (DIPTERA, PHORIDAE)

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ABSTRACT.   The eggsac of the pirate spider, *Mimetus notius,* is described and compared with eggs of other members of the genus. The phorid fly egg predator, *Phalacrotophora epeirae,* was reared from a *M. notius* eggsac.

Keywords: *Mimetus notius,* egg sac, *Phalacrotophora epeirae,* predation

Members of the family Mimetidae have justifiably earned the common appellations of "assassin" and "pirate" spiders because of their interesting feeding habits. Armed with a series of long, slightly curved spines on the promarginal areas of the tibiae and metatarsi of legs I and II (Kaston 1981), they enter spider webs, especially those of comb-footed spiders (Theridiidae) and orbweavers (Araneidae), and prey upon the occupants (Gertsch 1979). Jackson & Whitehouse (1986) observed mimetids using vibratory aggressive mimicry to lure spiders within striking range.

Although these spiders are poorly represented in systematic collections, a recent survey of the genus *Mimetus* Hentz 1832 in Kansas has revealed the presence of four species (Guarisco & Mott 1990). *Mimetus notius* Chamberlin 1923 is the second most commonly encountered member of the genus in northeastern Kansas. It has been taken in sweep samples of understory vegetation, mostly coralberry (*Symphoricarpos orbiculatus* Moench.), in woodland on the Fitch Natural History Reservation (FNHR) and on the eaves and outer walls of Reservation Headquarters (FNHR) in Douglas County, Kansas. The FNHR is a 590 acre (239 ha) tract of land which comprises all but the southwestern 50 acres (20 ha) of Section 4 (T12S, R20E) in Douglas County. It is located at the ecotone between the Eastern Deciduous Forest and Tallgrass Prairie Biomes, and ranges from 880–1080 feet (268–329 m) in elevation (39°00′, 95°11′) (Fitch & Kettle 1988). Two adult females were collected from eastern red cedar (*Juniperus virginiana* L.) in Montgomery and Greenwood counties, on 4 and 26 May 1991, respectively.

The egg sac of *M. notius* is fluffy, translucent, spherical to subspherical, and is composed of a 1 mm thick outer layer of sparse, curly, brown silk strands surrounding a dense white central section containing the brown eggs. Completely surrounding the egg sac is a thin, subspherical to elliptical net of silk. The egg sac is suspended within this net by several thick silk strands which extend from the sac to the net (Fig. 1). The shape of the net appears to be determined by the amount of space available near the egg sac. Two sacs, each laid within the confines of a petri dish, were surrounded by elliptical silk nets, 30 × 23 and 50 × 20 mm in diameter. Each net was 15 mm in height, which equalled the height of the petri dish. An egg sac discovered on the underside of a wooden door leaning against the outer wall of a laboratory building on the FNHR had a silk net with the following dimensions: 30 × 30 × 7 mm. Several egg sacs located in the corners between the eaves and outer walls of buildings possessed nets with similar dimensions.

A female collected on 4 May produced an egg sac 7 × 5 mm on 16 May containing 24 eggs. On 26 May, this individual produced a second egg sac (6 × 8 mm) containing an undetermined number of eggs. A second female obtained on 26 May produced a total of 5 egg sacs during the following four weeks. The first
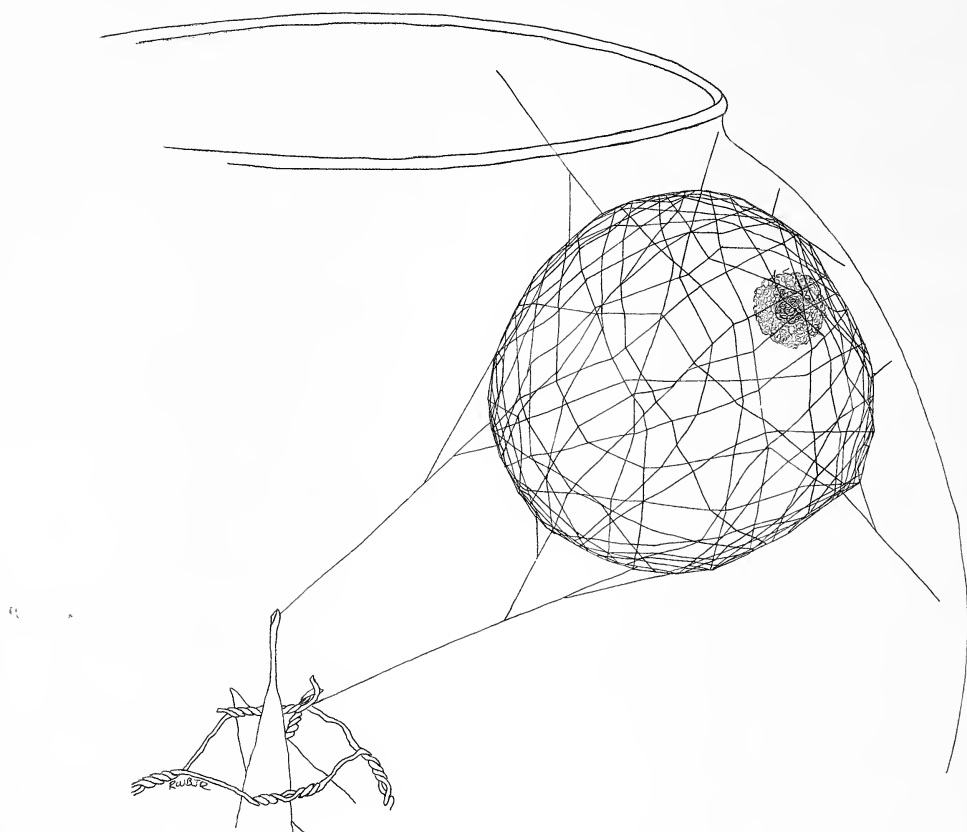
Figure 1.—*Mimetus notius* egg sac.

two egg sacs were laid on 28 May and 6 June, were 6 × 6 and 5 × 6 mm in diameter, with surrounding nets 20 and 25 mm in diameter, and contained a total of 29 and 37 eggs, respectively. The last three sacs were laid on 13, 21 and 27 June and contained 21, 12, and 25 eggs, respectively. These sacs were laid in a small vial, and the silk nets surrounding them were 15 × 25 mm. The last two egg sacs were probably infertile because they became covered with mold in a few days.

Observing the structure of egg sacs produced in the laboratory enabled me to recognize them in the field. One egg sac discovered on the FNHR on 18 June yielded 47 spiderlings ten days later. An egg sac collected from the eaves of a building in the Topeka Zoo on 21 June produced 35 spiderlings and one infertile egg on 4 July. Two egg sacs collected from the eaves of a residence in Lawrence, Douglas County, on 13 August contained 14 empty shells and 12 infertile eggs, and 25 empty shells and 7 infertile eggs, respectively.

The average number of eggs per sac = 28.9, SD = 9.71 (n = 10).

On 3 July, I collected a *M. notius* egg sac from the eaves of a house in Jefferson County, Kansas which contained several brown phorid fly pupae. Two days later, an adult fly, *Phalacrotophora epeirae* (Brues 1902)(Diptera, Phoridae), emerged from the egg sac. The remaining flies matured over the next few days.

The structure of the egg sac of *M. notius* resembles those of other members of the genus, except for the unique net of silk which surrounds it. *Mimetus puritanus* Chamberlin 1923 and *M. hesperus* Chamberlin 1923 both construct spherical, bright orange, loosely woven egg sacs (Guarisco & Mott 1990; Icenogle 1972). Lawler (1972) described the egg sacs of both wild and captive *M. eutypus* Chamberlin & Ivie 1935. They were loosely woven and those produced in captivity ranged from white to dark rust-brown, while the wild egg sacs were all pale yellow-white. The egg sacs of Old World mimetids are generally globular

with many loops of silk on the surface and contain only 5–20 eggs (Heimer 1986). The tufted nature of the silk may protect the eggs from mechanical damage, predation, or parasitism. Although it is tempting to speculate upon the probable functions of the unique structure of the egg sac of *M. notius*, further observations are needed to explore the relationships of various aspects of egg sac design and relative survivability.

The present observation on the emergence of *Phalacrotophora epeirae* from an egg sac of *M. notius* is the first recorded instance of egg predation or parasitism upon any member of the genus *Mimetus*. *Phalacrotophora epeirae* is a well known larval egg predator which has been reared from spider egg sacs of the following species: Linyphiidae: *Pityohyphantes costatus* (Hentz 1850)(see Manuel 1984); Araneidae: *Larinioides* Caporiacco 1934 (= *Nuctenea* Simon 1864 = *Epeira* Walckenaer 1805) sp. (see Brues 1902, 1903), *Larinioides sclopetarius* (Clerck 1757) (see Auten 1925), *Gasteracantha cancriformis* (Linnaeus 1785) (see Muma & Stone 1971); and Salticidae: *Phidippus audax* (Hentz 1845) (see Jones 1940).

ACKNOWLEDGMENTS

LITERATURE CITED

Auten, M. 1925. Insects associated with spider nests. Annals of the Entomological Society of America 18:240–250.

Brues, C.T. 1902. Notes on the larvae of some Texan Diptera. Psyche 9:351–354.

Brues, C.T. 1903. A monograph of the North American Phoridae. Transactions of the American Entomological Society 29:331–404 + 5 pl.

Fitch, H.S. & W.D. Kettle. 1988. Kansas Ecological Reserves (University of Kansas Natural Areas). Transactions of the Kansas Academy of Science 91(1–2):30–36.

Gertsch, W.J. 1979. American Spiders (second edition). Van Nostrand Reinhold, New York. 274 pp.

Guarisco, H. & D.J. Mott. 1990. Status of the genus *Mimetus* (Araneae: Mimetidae) in Kansas and a description of the egg sac of *Mimetus puritanus* Chamberlin. Transactions of the Kansas Academy of Science 93(3–4):79–84.

Heimer, S. 1986. Notes of the spider family Mimetidae with description of a new genus from Australia (Arachnida, Araneae). Entomologische Abhandlungen des Staatlichen Museums für Tierkunde in Dresden 49(7):113–137.

Icenogle, W.R. 1972. Notes on the biology of the genus *Mimetus*. Notes on Arachnology of the Southwest 3:19.

Jackson, R.R. & M.E.A. Whitehouse. 1986. The biology of New Zealand and Queensland pirate spiders (Araneae, Mimetidae): Aggressive mimicry, araneophagy and prey specialization. Journal of Zoology (London)(A) 210:279–303.

Jones, S.E. 1940. An annotated list of the spiders of an East Central Illinois forest (Wm. Trelease Woods, University of Illinois). Transactions of the Illinois Academy of Science 33(2):216–220.

Kaston, B.J. 1981. Spiders of Connecticut (revised ed.). State Geology and Natural History Survey of Connecticut, Bulletin. No. 70. 1020 pp.

Lawler, N. 1972. Notes on the biology and behavior of *Mimetus eutypus* Chamberlin and Ivie (Araneae: Mimetidae). Notes on Arachnology of the Southwest 3:7–10.

Manuel, R.L. 1984. The egg sac of *Pityohyphantes costatus* (Hentz) (Araneae, Linyphiidae) and its phorid parasite. Journal of Arachnology 12:371–372.

Muma, M.H. & K.J. Stone. 1971. Predation of *Gasteracantha cancriformis* (Arachnidae [sic]: Araneidae) eggs in Florida citrus groves by *Phalacrotophora epeirae* (Insecta: Phoridae) and *Arachnophaga ferruginea* (Insecta: Eupelmidae). Florida Entomologist 54(4):305–310.

SHORT COMMUNICATION

REVIEW OF THE SOUTH AMERICAN SPECIES OF THE GENERA *AULONIA* AND *ALLOCOSA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. *Aulonia bergi* (Holmberg 1876) and *Aulonia macrops* Simon 1897 are considered *nomina dubia*. *Agalenocosa luteonigra* (Mello-Leitão 1945) new combination (= *Aulonia luteonigra* Mello-Leitão 1945) is illustrated. *Glieschiella senex* (Mello-Leitão 1945) is illustrated and synonymized under *Allocosa brasiliensis* (Petrunkevitch 1910).

RESUMEN. *Aulonia bergi* (Holmberg 1876) y *Aulonia macrops* Simon 1897 se consideran *nomina dubia*. *Agalenocosa luteonigra* (Mello-Leitão 1945) nueva combinación (= *Aulonia luteonigra* Mello-Leitão 1945) se ilustra. *Glieschiella senex* (Mello-Leitão 1945) se illustra y sinonimiza bajo *Allocosa brasiliensis* (Petrunkevitch 1910).

Keywords: Araneae, Lycosidae, *Aulonia, Allocosa, Glieschiella*

Twenty-five species from South America were originally listed in the subfamily Hippasinae (Roewer 1954; Capocasale 1982, 1990). Originally I assigned 16 of these species (Capocasale 1990) to three different subfamilies according to the definitions given by Dondale (1986) for each subfamily. However, there are four taxa for which the systematic position is unknown. They are: *Allocosa senex* (Mello-Leitão 1945) and the three species of *Aulonia* from South America. The purposes of this note are to convey the results of the study of those four taxa and to clarify their systematic position. In this form the author completes his review of the lycosoid subfamily Hippasinae from South America.

Abbreviations used: MACN = Museo Argentino de Ciencias Naturales, Argentina; MLP = Museo de La Plata, Argentina; MHNP = Museum National d'Histoire Naturelle, Paris; MNRJ = Museu Nacional de Rio de Janeiro, Brazil. Illustrations were made with the aid of a camera lucida.

Aulonia bergi (Holmberg 1876)

Lycosa (Aulonia) Bergii Holmberg 1876: 176.
Aulonia gergi (sic): Bonnet 1955: 822.
Aulonia bergi: Mello-Leitão 1944: 321; Roewer 1954: 234

Comments.—Mello-Leitão (1944) considered *A. bergi* as a *nomen nudum*. Holmberg's description is: . . ."tomada en Las Conchas, y muy semejante a *Aulonia albimana* K. pero de doble longitud." Holmberg's types are lost; consequently it is impossible to make any definitive identification. As I cannot identify this species I consider it as a *nomen dubium*.

### *Aulonia macrops* Simon 1897

Aulonia macrops Simon 1897: 329, 1898: 30; Roewer 1954: 234; Lehtinen & Hippa 1979: 21.

Comments.—Lehtinen & Hippa (1979) considered this species as a Lycosinae and not congeneric with *Aulonia albimana*. I have examined the female holotype from Rio de Janeiro, Brazil, deposited at MHNP. It is immature. I agree with Lehtinen & Hippa that this specimen could be a Lycosinae, but I cannot identify it as *Aulonia*. I consider it as a *nomen dubium*.

Agalenocosa luteonigra (Mello-Leitão 1945) new combination
Figs. 1–7

Aulonia luteonigra Mello-Leitão 1945: 247; Roewer 1954: 234.
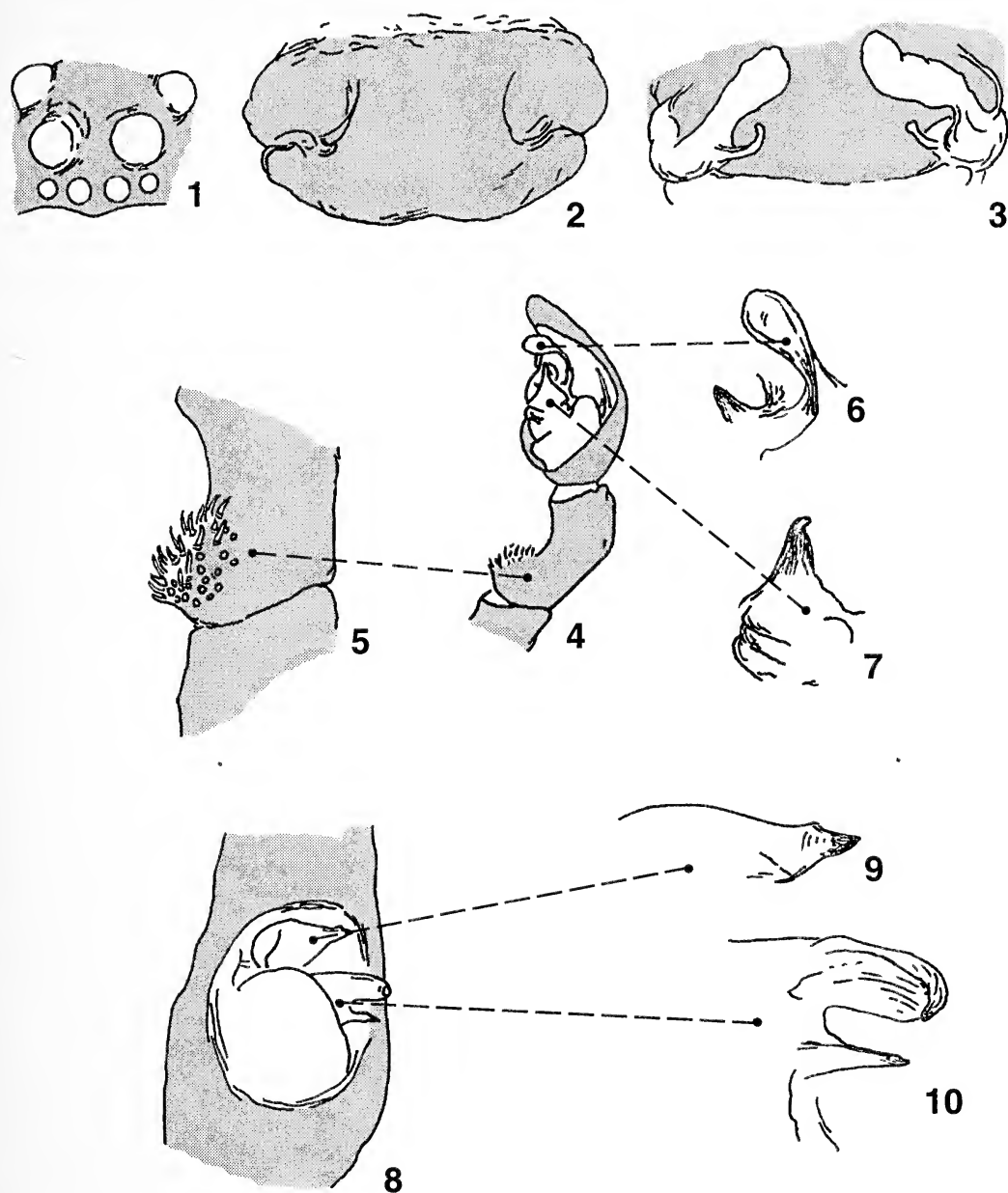
Figures 1–10. *Agalenocosa* and *Allocosa*. 1–7. *Agalenocosa luteonigra* (Mello-Leitão). 1. Eyes, frontal view; 2. Epigynum; 3. Spermathecae; 4. Palpus of male, ventral view; 5. Retrolateral apophysis of tibia, ventral view; 6. Terminal apophysis, ventral view; 7. Median apophysis, ventral view. 8–10. *Allocosa brasiliensis* (Petrunkevitch) (= *Glieschiella senex* Mello-Leitão, holotype MLP, Entre Ríos, Colón, Argentina); 8. Palpus of male, ventral view; 9. Terminal apophysis, ventral view; 10. Median apophysis, ventral view.

Comments.—Mello-Leitão (1945: 248) said the types are in MLP (N° 16480). However this number today does not exist in the collection of this museum. In this institution there is only an immature specimen (N° 16678) and two specimens without number (collection Birabén) one male and one female from Misiones, Pindapoy, Argentina. Although Pereira et al. (1999) suggest that they are syntypes, I cannot accept this conclusion. At MNRJ there are two specimens (a female and male) from Misiones, Pindapoy, Argen-

tina, labelled by Mello-Leitão as "typus." Judging by the measurements, etc., these are the holotype and female paratype.

The following apomorphic characters of *Aulonia luteonigra* Mello-Leitão—retrolateral apophysis in the male palpal tibia (Figs. 4, 5), terminal apophysis and lateral apophysis on the male palp (Figs. 4, 6, 7)—lead me to deduce that *A. luteonigra* share them with *Agalenocosa singularis* Mello-Leitão 1944 and *Agalenocosa punctata* Mello-Leitão 1944. For this reason, it must be established as a new combination.

Distribution.—Argentina: Misiones, Pindapoy; Santa María.

Specimens examined.—Six specimens: 1♂1♀ from Pindapoy, Argentina (holotype and female paratype) at MNRJ labelled by Mello-Leitão as "*typus*"; one immature from Misiones, Pindapoy, Argentina, at MLP (N° 16678) labelled by Mello Leitão; one male and one female from Misiones, Pindapoy, Argentina at MLP (collection Birabén) labelled by Mello-Leitão as "Cotipo"; one female from Argentina, Misiones, Santa María at MACN.

Allocosa brasiliensis (Petrunkevitch 1910)
Figs. 8–10

Moenkhausiana brasiliensis Petrunkevitch 1910: 223, figs. 26–29.
Allocosa brasiliensis: Capocasale 1990: 133.
Glieschiella senex Mello-Leitão 1945: 254. New synonym.

Comments.—The holotype is a male, not a female as Mello-Leitão said. I have examined this specimen from Entre Ríos, Colón, Argentina, deposited at MLP.

Capocasale (1990) synonymized *Glieschiella* Mello-Leitão 1932 and *Moenkhausiana* (Petrunkevitch 1910) with *Allocosa* Banks 1900; and since *Glieschiella halophila* Mello-Leitão 1932 and *Moenkhausiana argentinensis* Mello-Leitão 1938 were immatures he considered them *nomina dubia*. However, Capocasale (1990: 137) omitted this conclusion. Consequently, *Glieschiella senex* Mello-Leitão = *Allocosa senex* (Mello-Leitão); *Glieschiella alticeps* Mello-Leitão = *Allocosa alticeps* Mello-Leitão and *Moenkhausiana brasiliensis* Petrunkevitch = *Allocosa brasiliensis* (Petrunkevitch).

In this study the apomorphic characters, terminal apophysis and the median apophysis of the male palp (Figs. 8–10) of *Allocosa senex* confirm it is a new synonym of *Allocosa brasiliensis* (Petrunkevitch). Thus *Allocosa brasiliensis* (Petrunkevitch) and *Allocosa alticeps* (Mello-Leitão) are the only two good species.

LITERATURE CITED

Bonnet, P. 1955. Bibliographia Araneorum 2:1–918. Toulouse.

Capocasale R.M. 1990. Las especies de la subfamilia Hippasinae de América del Sur (Araneae,Lycosidae). Journal of Arachnology 18: 131–141.

Dondale, C. 1986. The subfamilies of wolf spiders (Araneae: Lycosidae). Actas X Congress International Aracnologia, Jaca/España 1:327–332.

Holmberg, E.L. 1876. Arácnidos Argentinos. Anales de Agricultura Argentina 4:1–30.

Lehtinen, P. & H. Hippa. 1979. Spiders of the Oriental-Australian region. I. Lycosidae: Venoniinae and Zoicinae. Annales Zoologica Fennici 16:1–22.

Mello-Leitão, C. 1944. Arañas de la Provincia de Buenos Aires. Revista del Museo de La Plata (N.S.) (Zool. 3) (24):311–393.

Mello-Leitão, C. 1945. Arañas de Misiones, Corrientes y Entre Ríos. Revista del Museo de La Plata (N.S.) (Zool. 4) (29):213–302.

Pereira, L.A., C. Sutton & M.J. Ramírez. 1999. Catálogo de tipos de Araneae (Archnida) del Museo de La Plata 45 (113–114):77–100.

Petrunkevitch, A. 1910. Some new of little known American spiders. Annals of the New York Academy of Science 19:205–224.

Roewer, C. 1954. Katalog der Araneae von 1788–1954. 2a:1–923. Verlag von Natura. Bremen.

Simon, E. 1897. Histoire naturelle des Araignées 2(2):1–380. Enc. Roret. Paris.

Simon, E. 1898. Description d'Arachnides nouveaux des familles des Agelenidae, Pisauridae, Lycosidae et Oxyopidae. Annales de la Societe Entomologique du Belgique 42:5–34.

SHORT COMMUNICATION

HARVESTMEN AS COMMENSALS OF CRAB SPIDERS

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ABSTRACT. Harvestmen *Phalangium opilio* regularly feed upon the carcasses of bees and moths discarded by crab spiders *Misumena vatia* Clerck 1757 hunting on flowers. I report one observation of a harvestman unsuccessfully attempting to secure a bee still being fed on by a crab spider.

Keywords: *Phalangium opilio*, *Misumena vatia*, Opiliones, scavenger, kleptoparasite

Harvestmen (Opiliones) are important consumers that feed upon a wide variety of animal and vegetable items, including both dead and live small invertebrates (Bishop 1949; Cloudsley-Thompson 1968). Although largely confined to the understory and litter during sunny conditions, a consequence of their limited ability to withstand desiccation (Bishop 1949; Cloudsley-Thompson 1968), harvestmen may wander widely over the vegetation, including large flowers and inflorescences, at night and at other times of high humidity (Todd 1949; Edgar 1971). The latter sites, such as inflorescences of common milkweed *Asclepias syriaca* also attract many insects, as well as their predators, one of the most common in northeastern North America being the crab spider *Misumena vatia* Clerck 1757 (Araneae: Thomisidae), a sit-and-wait predator (Morse 1981). Adult female *M. vatia* capture large prey, including bumble bees, honey bees, wasps, and noctuid moths (Morse 1986). Since the spiders feed without masticating these prey, the released carcasses drop intact, frequently lodging on lower parts of the vegetation in the process and providing a resource for scavengers. In our study site, an old field in Bremen, Lincoln County, Maine, USA (Morse 1981), these discarded carcasses sometimes accumulated on the broad milkweed leaves below the inflorescences, often remaining there for several days. However, when collecting carcasses for an unrelated analysis (Fritz & Morse 1985), we noted that many of them disappeared within a day of being dropped by the spiders, even during clear, calm periods when they were unlikely to be blown away by wind or washed off by rain. A few of these carcasses were also dismembered, probably where they had been dropped. These observations suggested the work of harvestmen, since harvestmen often carry food items away from a site and also process

large items by dismembering them (Cloudsley-Thompson 1968; Edgar 1971). Also, the harvestman *Phalangium opilio* Linnaeus 1758 (Phalangiidae, Palpatores) commonly visited flowering milkweeds in the study area during the night (recorded on 42.7% of censuses between 2100–0130 h of 100 inflorescences over a 10 year period, $n = 157$, unpubl. data).

To establish why these carcasses disappeared quickly, we collected eight sets of eight carcasses ($n = 64$) discarded by *M. vatia*, dusted them with red micronite dye, placed them under milkweed stems in the middle of the study site at three-day intervals (one set for each interval) and monitored them. Sixty of the 64 dyed carcasses were partly or totally dismembered or removed on the night after they were placed in the field. In 10 instances we subsequently found dyed carcasses, or parts of them, as high as 45 cm above the ground on leaves of the milkweed plants, and as far as 95 cm away from where we had placed them, indicating that they had been actively carried there. Edgar (1971) reported that harvestmen might carry food to sites of low disturbance, including tree trunks. Using pitfall traps, we subsequently captured seven *P. opilio* with mouthparts and facial regions covered by red dye, which they could have obtained only from the insect carcasses. Ants (Formicidae), the other important scavengers in the study area, were unlikely to have removed or processed the carcasses because the carcasses were manipulated only at night. Ant activity in this area is largely diurnal (Fritz & Morse 1981).

To explore the scavenging habits of *P. opilio* further, we confined 12 of them in 4-liter glass containers, one per container, and presented them with discarded spider prey. All fed heavily on these carcasses, in the process tearing them into smaller

parts similar to those found near the sites of the "food" caches and on the lower leaves of the milkweed. Nine of the 12 attacked the carcasses during the day (164.4 ± 75.4 min after they were placed in the containers), while the remaining three attacked the carcasses during the following evening. The substantial lag time for exploitation of these carcasses in the field (none taken until the following evening) is thus probably a consequence of the low activity levels of harvestmen during the middle of warm, dry days, conditions not experienced in the shade and relatively high humidity of the laboratory.

Given the apparent high frequency of scavenging by the harvestmen, it is of interest to know whether they kleptoparasitize the spiders while the latter are feeding on their large prey, an act that could provide considerably larger rewards for the harvestmen than the spent carcasses. Here I report an observation of a *P. opilio* attempting to wrest control of the honey bee *Apis mellifera* prey of an adult female *M. vatia*. We made this observation under illumination of a battery-driven headlamp covered by a red filter. Neither the harvestman nor the spider showed any sign of being affected by the resulting red light. At 2125 h on 21 July 1982, shortly after darkness, we observed an adult *P. opilio* on an inflorescence of a common milkweed in full flower. Within this inflorescence, approximately 3 cm away, an adult female *M. vatia* was still feeding on a honey bee it had captured at 1430 h the preceding afternoon. Although the spider was largely buried within the flowers of the inflorescence, its prey was located on the outside of that inflorescence in a conspicuous and seemingly vulnerable position. The harvestman initially moved to the end of the bee opposite the spider (the bee's abdomen) and attempted to grasp it with its mouthparts three different times within a few seconds. Each time the spider responded aggressively to the approaches of the harvestman by rearing and rapidly moving its large forelimbs forward. In response, the harvestman quickly retreated backward for one to two bee lengths, simultaneously lowering its body so that it was situated immediately behind the bee. Rapidly following each thrust and retraction by the spider, the harvestman lunged forward in an apparent attempt to secure the bee carcass. In a final effort the harvestman quickly advanced on top of the bee, but during the rapid subsequent response by the spider the harvestman fell off the umbel and dropped into the grass about 80 cm below its previous location. We observed it there for 10 min; but it did not attempt to climb back up the plant, and eventually it wandered away from the plant.

Misumena vatia would be unlikely to take the harvestman as prey, although spiders are often listed as regular predators of harvestmen (Edgar 1971). We have never seen *M. vatia* with harvestman prey,

although logging thousands of hours of field observations on them in over 20 years (1977–2000), both by day and night, and documenting a wide variety of other prey taken by this spider (pers. obs.). Further, as implied, *P. opilio* is common in the study area and regularly recorded in censuses (unpubl. data). Therefore the danger inherent in this act, often cited as an important tradeoff of kleptoparasitism (Whitehouse 1997), seems low and unlikely to inhibit the harvestman's effort to secure the food item. In common with other Palpatores, *P. opilio* possesses large, anterolateral exocrine glands (Bishop 1949), which contain noxious secretions that appear to deter many potential predators (Edgar 1971). However, we have found the brown crab spider *Xysticus emertoni* Keyserling 1880, a far less frequent visitor to flowers than *M. vatia*, feeding on *P. opilio* (pers. obs.). *Xysticus emertoni* regularly feeds on putatively noxious prey that we have never seen *M. vatia* exploit (Morse 1983).

The ready exploitation of spent prey by *P. opilio* strongly suggests that the interaction between this harvestman and the spider was an extension of normal scavenger behavior, though the repeated attempts to wrest the bee carcass from the spider were consistent with predatory behavior by the harvestman. *Phalangium opilio* is well known to prey on small invertebrates (Bristowe 1949). Sabini & Gnaspini (1999) have recently reported an instance of a tropical gonyleptid species taking a moth from a ctenid spider hunting on a tree trunk, which they believe to be the first reported instance of kleptoparasitism by a harvestman. Nearly all instances of probable kleptoparasitism involving spiders have been reported from web-building species, probably because of the relatively high availability of prey there and the web owner's difficulty of patrolling all parts of large webs (Vollrath 1987; Cangialosi 1997; Grostal & Walter 1997).

As we have observed this interaction only once, it seems unlikely to be common, although it would not be observed routinely, given the time of day at which it occurred. It would appear unlikely to result in a major loss of resources to the spiders, especially if such attacks took place after the carcass had been almost completely processed, as in the present instance, when the spider had already retained the bee considerably longer than usual (Morse & Fritz 1982). Even then, the spider showed no tendency to give up its prey to the harvestman, so it remains unclear whether *P. opilio* would often succeed in appropriating such food items before they were discarded by their original exploiters. It thus seems premature to consider *P. opilio* to be a kleptoparasite of *M. vatia*. However, *P. opilio* clearly benefits as a commensal of *M. vatia*, obtaining a resource that would otherwise be unavailable to it.

LITERATURE CITED

Bishop, S.C. 1949. The Phalangida (Opiliones) of New York. Proceedings of the Rochester Academy of Science 9:159–235.

Bristowe, W.S. 1949. The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food. Journal of Animal Ecology 18:100–114.

Cangialosi, K.R. 1997. Foraging versatility and the influence of host availability in *Argyrodes trigonum* (Araneae, Theridiidae). Journal of Arachnology 25:182–193.

Cloudsley-Thompson, J.L. 1968. Spiders, Scorpions, Centipedes and Mites. Oxford: Pergamon.

Edgar, A.L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Miscellaneous Publications of the Museum of Zoology, University of Michigan 144:1–64.

Eisner, T., D. Alsop & J. Meinwald. 1978. Secretions of opilionids, whip scorpions and pseudoscorpions. Pp. 87–99. *In* Arthropod Venoms. (S. Bettini, ed.), Springer-Verlag, Berlin.

Fritz, R.S. & D.H. Morse. 1985. Reproductive success, growth rate and foraging decisions of the crab spider *Misumena vatia*. Oecologia 65:194–200.

Grostal, P. & D.E. Walter. 1997. Kleptoparasites or commensals? Effect of *Argyrodes antipodianus* (Araneae: Theridiidae) on *Nephila plumipes* (Araneae: Tetragnathidae). Oecologia 111:570–574.

Morse, D.H. 1981. Prey capture by the crab spider *Misumena vatia* (L.) (Thomisidae) on three common native flowers. American Midland Naturalist 105:358–367.

Morse, D.H. 1982. The turnover of milkweed pollinia on bumble bees, and implications for outcrossing. Oecologia 53:187–196.

Morse, D.H. 1983. Foraging patterns and time budgets of the crab spiders *Xysticus emertoni* Keyserling and *Misumena vatia* (Clerck) (Araneae: Thomisidae) on flowers. Journal of Arachnology 11:87–94.

Morse, D.H. 1986. Predatory risk to insects foraging at flowers. Oikos 46:223–228.

Morse, D.H. & R.S. Fritz. 1982. Experimental and observational studies of patch-choice at different scales by the crab spider *Misumena vatia*. Ecology 63:172–182.

Sabino, J. & P. Gnaspini. 1999. Harvestman (Opiliones, Gonyleptidae) takes prey from a spider (Araneae, Ctenidae). Journal of Arachnology 27:675–678.

Todd, V. 1949. The habits and ecology of the British harvestmen (Arachnida, Opiliones), with special reference to those of the Oxford district. Journal of Animal Ecology 18:209–229.

Vollrath, F. 1987. Kleptobiosis in spiders. Pp. 274–286. *In* Ecophysiology of Spiders. (W. Nentwig, ed.), Springer-Verlag, Berlin.

Whitehouse, M.E.A. 1997. The benefits of stealing from a predator: Foraging rates, predation risk, and intraspecific aggression in the kleptoparasitic spider *Argyrodes antipodiana*. Behavioral Ecology 8:663–667.

SHORT COMMUNICATION

DIFFERENCES IN THE ACTIVITY OF JUVENILES, FEMALES AND MALES OF TWO HUNTING SPIDERS OF THE GENUS *CTENUS* (ARANEAE, CTENIDAE): ACTIVE MALES OR INACTIVE FEMALES?

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ABSTRACT.   The difference in activity levels between adult male and female spiders has been attributed to a more sexually motivated searching behavior by males, but the possibility that females reduce their activity when they reach maturity has not been considered, which may be evaluated by comparing adults and late instar juveniles behavior. We recorded the displacements during 15 min periods for 137 males, females and juveniles of *Ctenus amphora* and *C. crulsi*, two similar-sized syntopic hunting spiders species which search for prey on the leaf litter in central Amazonian tropical rainforests. For both species, males were significantly more active than females and juveniles. *Ctenus amphora* females were less active than juveniles, but the *C. crulsi* female activity did not differ from the juvenile activity. There were no significant differences in activity between these species for males and females, but the juveniles of *C. amphora* where more active than the juveniles of *C. crulsi*. Therefore, differences in activity between sexes are not always restricted to changes in male behavior, and the degree of decrease in female activity may depend on how active juveniles are.

Keywords: Amazonia, behavior, movements, foraging mode

Hunting spiders actively move about in search of prey (Uetz et al. 1999). However, activity levels may differ between adult males and females (e.g., Schmitt et al. 1990). This difference has been attributed to a more sexually motivated searching behavior of males (Rovner & Barth 1981); but, as far as we know, the possibility that females reduce their activity when they reach maturity has not been considered. To test this hypothesis it is necessary to compare the behavior of adults with that of late instar juveniles. The objective of the present paper is to evaluate whether the differences in activity between sexes in two species of hunting spiders (*Ctenus amphora* Mello-Leitão 1930 and *C. crulsi* Mello-Leitão 1930) may be attributed to a more active behavior of adult males, a less active behavior of adult females, or both. Both species forage on the leaf litter, do not have fixed retreats, have similar size (both with prosoma length of 5.5–11 mm) and are sympatric in the study areas.

The observations were made in Adolfo Ducke Forest Reserve, a 10,000 ha "terra-firme" primary forest reserve 25 km north of the city of Manaus, Brazil, where the ecology of this genus has been intensively studied (Höfer et al. 1994; Gasnier 1996; Gasnier & Höfer 2001) and on the campus of the Universidade do Amazonas, a forest fragment in Manaus. Using head lamps, we observed the spiders during their nocturnal activity, in the dry (2 nights in June and 3 nights in October of 1998) and wet seasons (6 nights in January and 3 nights in April of 1999). We memorized the trajectory of the movements for 15 min of activity and recorded the total displacement (including curves) with a tape measure. This was possible because of the low activity levels and the tendency of the spiders to move in straight lines. We tried to minimize the effect of our presence on the behavior of the spider by using a red filter on the lamp and by avoiding movements. Voucher specimens for these

studies are deposited in the arachnological collection of the Instituto Nacional de Pesquisas da Amazônia under the numbers INPA-001 to INPA-023. We used non-parametric statistics (Mann Whitney U-test and Kruskal-Wallis H-test), for all comparisons. Our significance level was $\alpha = 0.05$; however, we adjusted α when multiple comparisons were performed following Rice (1989). When we compared juveniles, males and females, we had three pairs of comparisons per species: in these cases, we used the significance levels of 0.017, 0.025 and 0.05 from the greatest to smallest P value.

We observed 137 *Ctenus crulsi* individuals (28♀, 19♂ and 37 juveniles) and *C. amphora* (15♀, 14♂ and 24 juveniles). There were no significant differences between the species in the displacements of males ($U_{14.19} = 136$, $P = 0.91$) (Fig. 1) or females ($U_{15.28} = 186$, $P = 0.44$). However, *C. amphora* juveniles were significantly more active than *C. crulsi* juveniles ($U_{24.37} = 579$, $P = 0.03$).

There were significant differences in displacement among males, females and juveniles within each species (*C. amphora:* $H = 14.45$, $P < 0.001$; *C. crulsi:* $H = 19.71$, $P < 0.001$). For both species, the males were significantly more active than females (*C. amphora:* $U_{14.15} = 176$, $P < 0.001$ and *C. crulsi:* $U_{19.28} = 436$, $P < 0.001$) and significantly more active than juveniles (*C. amphora:* $U_{24.14} = 94.50$, $P = 0.02$ and *C. crulsi:* $U_{37.19} = 143$, $P < 0.001$). However, the species differed when we compared the activity of females and juveniles. *Ctenus amphora* females were significantly less active than juveniles ($U_{24.14} = 267$, $P = 0.01$), and *C. crulsi* female activity did not differ from juvenile activity ($U_{37.28} = 564.50$, $P = 0.48$).

Our results support the hypothesis that males become more active when they reach maturity. However, at least for *C. amphora*, females activity does decline. The reason for this, and for the absence of a decline in *Ctenus crulsi*, is not clear. Gasnier (1996) found no evidence that these species differed in reproductive cycle and apparently they reproduce continuously throughout the year, so males probably seek females in all seasons. Extreme sedentary behavior appears to be the foraging strategy adopted by adult females of this genus. However, juveniles of these species have different foraging strategies and this may re-
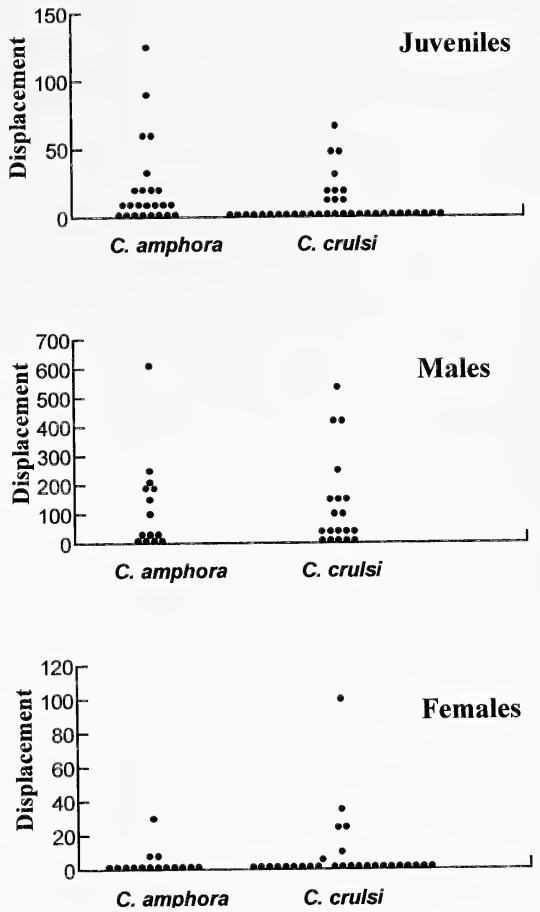

Figure 1.—Displacement (cm) of juveniles and adults of *Ctenus amphora* and *Ctenus crulsi* during a 15 minute period.

sult from differences in the species' diets and the resources available. It will be necessary to study diet and resource availability to determine whether these factors affect the activity of males, females and juveniles of these species, and why some females become less active and others maintain the same level of activity as juveniles.

LITERATURE CITED

Gasnier, T.R. 1996. Ecologia comparada de quatro espécies de aranhas errantes do gênero *Ctenus* (Walckenaer) (Araneae, Ctenidae) em uma flo-

resta na Amazônia Central: Bases para um modelo integrado de coexistência. Dr. Thesis, CAPES/INPA/FUA. Manaus, Brasil. 77 pp.

Gasnier, T.R. & H. Höfer. 2001. Patterns of abundance of four species of wandering spiders (Ctenidae, *Ctenus*) in a forest in central Amazonia. Journal of Arachnology 29:95–103.

Höfer, H., A.D. Brescovit & T. Gasnier. 1994. The wandering spiders species of the genus *Ctenus* (Ctenidae, Araneae) of Reserva Ducke, a rainforest reserve in central Amazonia. Andrias 13: 81–98.

Rice, W.R. 1989. Analysing tables of statistical tests. Evolution 43:223–225.

Rovner, J.S. & F.G. Barth. 1981. Vibratory communication through living plants by a tropical wandering spider. Science 214:464–466.

Schmitt, A., M. Schuster & F.G. Barth. 1990. Daily locomotor activity patterns in three species of *Cupiennius* (Araneae, Ctenidae): The males are the wandering spiders. Journal of Arachnology 18:249–255.

Uetz, G.W., J. Halaj & A.B. Cady. 1999. Guild structure of spiders in major crops. Journal of Arachnology 27:270–280.

BOOK REVIEW

Forest Spiders of South East Asia. Christa L. Deeleman-Reinhold. 2001. K. Brill NV. Leiden, The Netherlands. *xii* + 592 pages. ISBN 90-04-11959-0. US$200. (US and Canadian orders to cs@brillusa.com)

The title of this book suggests a broad coverage of the south east Asian fauna, but the subtitle quickly reveals that its main subject matter is a revision of just six families from the area. Whether additional volumes on other families are projected is not stated.

The book is well made, the printing, paper and binding all of high quality, print clear and easily readable, illustrations well laid out and of generous size, and distribution maps (50 of them) large and clear. The author is to be complimented on this culmination of 20 years of research in many parts of south east Asia.

An introductory section of 26 pages deals briefly with objectives, definition of the area covered (Thailand, Malaysia, and Indonesia exclusive of Irian Jaya), history of araneology of the area, some aspects of spider natural history, taxonomy and zoogeography, and methods of collecting and study. A six page glossary follows the introduction and is succeeded by a 40 page illustrated key to araneomorph spider families (liphistiids and mygalomorphs are keyed only to order-group level). The key runs to only 48 couplets, 33 of the 40 pages are taken up by 131 figures. (These figures are numbered separately from and in addition to the figures in the revisionary section.)

The bulk of the book, almost 500 pages, consists of a study of the forest spiders of six families – Clubionidae, Corinnidae, Liocranidae, Gnaphosidae, Prodidomidae and Trochanteriidae. A seventh family, Miturgidae, is mentioned only to be dismissed as not occurring in south east Asia. (The author has returned the Butichurinae to the family Clubionidae.)

A new subfamily, 18 new genera and over 100 new species are described, the great majority of them in the first three of the families listed above. The illustrations (989 of them)

are mostly of palps and epigyna or habitus (minus legs or legs shown on one side), with various other structures shown as appropriate.

Lists of species from other tropical Asian areas are presented, and unidentified specimens are mentioned with brief notes, and shown on the distribution maps. Occasional genera from outside the area are included. The author states that "type species of all genera ostensibly present in the tropical Asian region have been included."

Diagnoses and descriptions are given for both new and previously described taxa. The species descriptions include primarily measurements, short notes on coloration, cheliceral teeth, leg spination and special structures such as abdominal scuta. Genital structures are discussed largely in the diagnoses. Other information includes collection data, type locality, habitat, distribution and (usually) etymology of new names. The taxonomic section is followed by acknowledgements (two pages), a list of arachnological periodicals and societies (one page), a list of references (six pages), index (nine pages), and eight photographic color plates with 19 illustrations, including the remarkable ant-mimicking corinnid *Pranburia*.

This is, so far as I know, the first and only high-quality major taxonomic work on south Asian spiders so far produced. The author is surely to be congratulated on a huge job well done. The criticisms below (and some criticisms are always called for by a work of this size) do not detract significantly from the work.

The most obvious, and at first rather jarring, defect is in the illustrations, a large number of which are quite noticeably asymmetrical. Producing symmetrical drawings can be difficult, but a simple trick solves the problem. (Some

specimens, of course, really are asymmetrical, but they are few.) Details seem fuzzy in some drawings, but this cannot be judged properly without comparison with specimens.

There are frequent minor errors of spelling and grammar, and awkwardnesses, of English usage. I assume this results from the author's writing in what is not her first language. The publisher should bear some of the responsibility for this.

Two terms used frequently in the text activate two of my pet peeves. The words "chitinized" and "sclerotized" are both used for describing hard and rigid structures. Chitinized is not appropriate for this meaning, though it was commonly so used in older literature. Chitin is a soft, flexible substance. Hardening is by sclerotization. The term "vulva" is used for internal female genitalic structures, a common usage in Europe, but entirely inappropriate. The word vulva, simply transferred from vertebrate anatomy, refers specifically to *external*, not internal structures. I see no problem in simply referring to the whole secondary genitalic apparatus, external and internal, as the epigynum, and referring to, e.g., "ventral view" and "dorsal view, cleared."

It is astonishing to have two major works on tropical Asian spiders appear nearly simultaneously, especially two so well done. This volume, in conjunction with Frances and John Murphy's, should surely stimulate interest in south east Asian spiders. It is unfortunate that the very high price of the present volume will probably severely limit its availability. The contrast in prices of the two works could scarcely be greater.

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BOOK REVIEW

An Introduction to the Spiders of South East Asia, With Notes on All the Genera. Frances and John Murphy. 2000. Malaysian Nature Society, P.O. Box 10750, 50724 Kuala Lumpur, Malaysia, vii + 625 pp., *ca.* US$34 (yes, $34!) plus postage.

This is a most remarkable book, quite unlike anything previously produced on spiders. It isn't exactly a field guide, although it contains over 250 color images of spiders taken by one of the most talented photographers ever to grace our field, Frances Murphy, and its discussions of taxa are organized in ways to make them maximally useful to collectors and field biologists. It isn't exactly an identification manual, even of the *"How to Know the Spiders"* ilk, for there are no dichotomous keys (or genitalic illustrations for species identification) to be found anywhere between its covers. But it is exactly what the title indicates – a superb introduction to the spiders of a significant chunk of the world.

That chunk is somewhat curiously defined; the book covers, as one would expect, Vietnam, Cambodia, Laos, Thailand, and Myanmar. But it also covers Sumatra, Java, Borneo, and even the Philippines. Even more surprisingly, a large part of southern China, and Taiwan, are included (although the authors admit that, in retrospect, some of the Chinese provinces covered have faunas with more northern affinities and don't fit well).

In any case, the volume will be of interest to arachnologists everywhere, for it includes a number of unique features. Perhaps most obvious is the plethora of habitus drawings; I doubt that there is any other work that includes so many fine drawings of the entire bodies of such a varied cast of characters (many of these drawings are by the world-renowned spider illustrator Michael Roberts, and were especially commissioned for the book). In some cases, these are probably the first habitus drawings ever to appear for given taxa (such as the family Cithaeronidae).

Also unique is the organization, especially in the treatments of the larger families. Take, for example, the araneids. First discussed are a number of rare genera that include only one or two species; in most cases, no information on these taxa has appeared since their original description (often a century ago), and little can be said about these animals. For more modern taxa, likely errors are often pointed out; so, for example, a Chinese species described in the New World genus *Eustala* in 1990 is suggested to be closer to *Cyclosa* instead (and in this case, a transfer of the species to that genus has actually been published, in an obscure Chinese journal).

For the genera more likely to be recognized, the treatments are arranged by where the spiders' webs are most likely to be found: on vegetation, on dead twigs or bare branches, or at the ground layer. One genus, the curious *Chorizopes*, is even separated out as being found in leaf litter – I was not aware of that, or that these spiffy animals spin no webs and instead prey on other spiders! The authors have spent a considerable amount of time collecting and observing spiders in southeast Asia, and the book is chock-full of such tidbits of natural history information. For that reason, as well as an often delightfully sly turn of phrase, even the most detailed parts of the text are quite readable. With regard to *Cithaeron*, for example, we're told that "When disturbed, their main defence against even the most experienced collectors is an unreasonable turn of speed."

As introductory material, to help newcomers to the field, the book includes brief accounts of the other arachnid orders (even those which don't occur in southeast Asia),

spider anatomy, natural history, and collecting techniques. The liphistiids, mygalomorphs, and araneomorphs are treated separately; but within the two large infraorders, the families are listed alphabetically, which leads to some strange juxtapositions (anapids are thus found between amaurobiids and anyphaenids, rather than with mysmenids or symphytognathids). But tables of "field hints for families" will help the novice navigate through this huge compendium of information.

After the family discussions, there is a full checklist of species recorded from the area, comprising over 80 pages, with detailed geographic data. The bibliography is extensive (another 35 pages), and there are useful lists of societies, periodicals, a glossary, and a detailed index. The book is capped by 32 gorgeous color plates of photographs, mostly by Frances Murphy. Those of us fortunate enough to have known Frances regret immensely that she did not survive to see this publication, but it is a most impressive tribute to her unflagging enthusiasm, and to her desire to communicate that enthusiasm to others. Indeed, as John Murphy aptly phrases it, he "became an arachnologist by marriage" (a fate with which I can readily sympathize, since I became one by courtship instead)!

As with any project this large, there are always items about which one could carp (*Cyclocosmia* is known from Thailand as well as China; the accounts of *Crassignatha* on pp. 83 and 221, for example, imply that there is some controversy about the family-level relationships of the genus, when there is only a difference in the relative ranking of groups involved). But, on the whole, typographical and other errors are quite uncommon, and they fade into total insignificance when one considers that this enormously useful volume has been made available at a price that seems impossibly low. There is surely no better bargain to be had, for the selling price is an entire order of magnitude lower than that of some similarly large volumes! For this feat, both the authors and the publisher (Mr. Henry Barlow of the Malaysian Nature Society) are to be congratulated heartily (potential purchasers may wish to contact Mr. Barlow at hsbar@pc.jaring.my, or P.O. Box 10139, 50704 Kuala Lumpur, for details on exchange rates, postage options, and payment methods). I suspect that the inexpensive availability of such a remarkably useful volume will lead to a substantial increase in interest in, and work on, the southeast Asian arachnid fauna, and in the end, there could be no more appropriate tribute to Frances Murphy than that!

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INSTRUCTIONS TO AUTHORS

(revised August 2000)

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 1–4.—*A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us* holotype male; 33, 34. *A-us y-us* male. Scale = 1.0 mm.

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CONTENTS

The Journal of Arachnology

The Journal of
ARACHNOLOGY

Cover photo: Western Black widow, *Latrodectus hesperus*, molting. From New Mexico. Photo by Bryan E. Reynolds.

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⊗ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

GROSS MUSCULAR ANATOMY OF *LIMULUS POLYPHEMUS* (XIPHOSURA, CHELICERATA) AND ITS BEARING ON EVOLUTION IN THE ARACHNIDA

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ABSTRACT. Due to their widespread use as model systems and their reputation as living fossils, horseshoe crabs (Xiphosura) have been studied intensively by physiologists and paleontologists. The close phylogenetic relationship between horseshoe crabs and arachnids might also have been expected to inspire studies of xiphosurans by comparative arachnologists, but surprisingly few have been undertaken. Here, the first exhaustive survey of muscular anatomy of the Atlantic horseshoe crab is conducted as part of an on-going study of the evolutionary morphology and phylogeny of arachnids. Dissections of adult and immature individuals established 113 muscle groups comprising over 750 individual muscles, with several being recognized or correctly described for the first time. New insights into skeletomuscular evolution and phylogeny of arachnids were derived primarily from the axial muscle system. Specifically, it is argued that *Limulus* retains a box-truss axial muscle system like that of plesiomorphic members of other arthropod groups, that this is also a plesiomorphic condition for Chelicerata, and that arachnids are united by the loss of one component of this system, the anterior oblique muscles. Combined with comparative morphological and molecular evidence from previous studies, this study adds greater weight to the widely held view that, among extant chelicerates, Xiphosura and Arachnida are monophyletic sister groups and counters recent speculation that scorpions are more closely related to xiphosurans than to spiders, whipscorpions and other arachnids.

Keywords: Horseshoe crab, morphology, phylogeny, muscles

Due to its large size, availability to investigators and reputation as a "living fossil," the Atlantic horseshoe crab, *Limulus polyphemus* (Linneaus 1758) (Xiphosura, Chelicerata), is one of the most intensively studied invertebrates (e.g., Cohen 1979; Bonaventura et al. 1982; Sekiguchi 1988), and aspects of its external and internal anatomy are routinely depicted in textbooks. Investigations of its skeletomuscular anatomy were undertaken repeatedly in the nineteenth and early twentieth centuries (e.g., Milne-Edwards 1873; Owen 1873), with the works of Lankester (1881, 1885; Lankester et al. 1885) and Patten (1893, 1912; Patten & Redenbaugh 1899–1900; Patten & Hazen 1900) being the most influential. Lankester's work led to the conclusion that *Limulus* is a chelicerate (originally "arachnid") rather than a crustacean, and subsequent workers have tended to adopt his terminology and muscle numbering system (e.g., Snodgrass 1952; Manton 1964; Wyse & Dwyer 1973). Although Patten's studies generally surpassed Lankester's in quality and detail, the reputation of Patten's

descriptive work may have suffered from its association with his failed attempt to demonstrate the origin of vertebrates from chelicerates (Patten 1912). Later workers often based their phylogenetic and functional inferences on these early descriptions (e.g., Versluys & Demoll 1922; Størmer 1944; Fage 1949; Manton 1964; Wyse & Dwyer 1973), and cursory empirical work has tended to corroborate the classic treatments.

Despite the influence of the early anatomical studies, important discoveries were made whenever detailed exploratory surveys were undertaken, especially those focusing on embryonic or larval stages. For example, Iwanoff (1933) showed the chilaria in *Tachypleus gigas* (Müller 1785) (formerly *Limulus moluccans*) to be appendages of postoral somite VII and refuted morphological speculations of Versluys & Demoll (1922), who hypothesized the derivation of xiphosurans from arachnids. Scholl (1977) showed that the dorsal hinge between the cephalothorax and abdomen is a tergal specialization of postoral somite VIII, discovered muscles associated with the pedal

coxae inserting on the walls of the preoral chamber, and showed that postoral somite I (cheliceral somite) migrates rearward during ontogeny and thereby distorts the metameric pattern in the adult. Interestingly, most of these features are also evident in adults and subadults and, as demonstrated here, would have been revealed by more detailed descriptions of these stages. Given that new skeletomuscular features have been discovered by each careful survey of skeletomuscular anatomy, and the absence of a single treatment encompassing all known skeletal muscles, I chose to undertake an exhaustive survey of skeletal muscles in *Limulus*, with the specific goal of integrating the resulting data with those obtained from original dissections of arachnids (Shultz 1993, 1999, 2000).

The present survey documents 113 muscle groups which encompass over 750 individual muscles. Most have been described in earlier studies, but several evolutionarily significant muscles were undescribed, described imprecisely or incorrectly, or described correctly in poorly known publications. These features include 1) two sets of three cheliceral muscles arising on the carapace that are generally depicted as one muscle; 2) four intrinsic cheliceral muscles; 3) a preoral sphincter elaborated from the coxosternal region of the prosoma; 4) muscles that originate on the coxae of legs 1–4 and insert on the preoral chamber; 5) extrinsic chilarial muscles; 6) muscles associated with the chondrites of the opisthosomal appendages (i.e., chilaria and opercula); 7) evidence that the axial muscles of the abdomen are homologous with the box-truss muscle system of other plesiomorphic arthropods; 8) evidence that the so-called "branchio-thoracic" muscles are axial muscles rather than extrinsic muscles of the opercula; 9) evidence that the first six pairs of dorsal endosternal suspensor muscles are members of a single metameric series rather than two different series; 10) thin, sheet-like ligaments connecting the ventral surfaces of the endosternite to the pliable intercoxal cuticle; and 11) the absence of the ventral esophageal dilator muscle described by Lankester et al. (1885). Combined with information currently available for arachnids, these and other new perspectives on the muscular anatomy of *Limulus* provide insights in the phylogeny and evolutionary morphology of arachnids. Notably, this information

confirms the widely held view derived from morphological and molecular evidence that Arachnida is monophyletic with respect to Xiphosura and contradicts recent proposals that scorpions are more closely related to xiphosurans than to other arachnids (e.g., van der Hammen 1989; Dunlop 1998).

METHODS

Preserved specimens of *Limulus polyphemus* were obtained from Ward's Natural Science Establishment, Inc. and Carolina Biological Supply Co. and ranged in mid-sagittal carapace length from 2–12 cm. Dissections were performed using a Leica M10 dissecting microscope at magnifications of 1× to 1280×. Only standard dissection equipment and techniques were used. Drawings were made with a drawing tube, scanned electronically and transformed into black-and-white bitmaps, which were then enhanced and labeled using a variety of graphics software.

RESULTS

This study does not provide a complete redescription of skeletomuscular anatomy *Limulus* but surveys the skeletal muscles in an attempt to 1) corroborate descriptions of earlier workers (i.e., Lankester et al. 1885; Patten 1912; Snodgrass 1952; Manton 1964; Scholl 1977), 2) clarify ambiguities and correct errors in earlier descriptions, 3) describe "new" features, and 4) document gross muscular anatomy in a manner comparable to descriptions being generated for other chelicerates (Shultz 1993, 1999, 2000). The "Results" section highlights novel observations, but a brief description of all muscles is provided in Table 1 and sources for detailed descriptions are provided in the text. Italicized Arabic numerals refer to the muscles listed in Table 1, and Roman numerals refer to postoral somites.

General anatomy.—The chelicerate body consists of two tagmata, prosoma and opisthosoma. The prosoma includes a preoral region and six embryologically postoral appendage-bearing somites (I-VI) (Damen et al. 1998; Telford & Thomas 1998). The primitive opisthosoma was probably composed of 11 or 12 somites and a terminal peri- or post-anal structure, the telson (Weygoldt & Paulus 1979; Shultz 1990; Anderson & Selden 1997). *Limulus* and other extant xiphosurans depart secondarily from this organization in several

ways. Specifically, the first opisthosomal somite (VII), along with its appendages (chilaria), and medial tergal elements of the second (VIII) are incorporated into the prosoma to form a "cephalothorax" (Scholl 1977) (Fig. 3B). The remaining opisthosomal somites are consolidated dorsally, laterally and posteriorly into a heavily sclerotized abdomen (Figs. 1, 2) which bears six opercular appendages (i.e., the anterior genital operculum with paired genital openings and lacking book gills and five opercula with book gills) inserted into a pliable ventral cuticle (Fig. 2). The hard dorsal surface of the abdomen is here termed the tergum and the hard posterior ventral surface is termed the postopercular sternum. There are seven well-defined opisthosomal somites (VIII-XIV) within the abdomen which are indicated by the arrangement of dorsal entapophyses (i.e., internal projections formed by invagination of the tergal exoskeleton), marginal spines, and appendages (Figs. 1, 3). There is internal evidence of another somite (XV) in the form of a crescent-shaped site of muscle attachment on the abdominal tergum (Fig. 1A: *36, 37*). The musculature of somite XV is more complicated in larval stages and resembles that of the more anterior abdominal somites but lacks a dorsal entapophysis (Scholl 1977: fig. 5).

Appendicular muscles.—The skeletomuscular anatomy of appendages in *Limulus* has been described by several workers, notably Lankester et al. (1885), Patten (1912), Vachon (1945), Snodgrass (1952), Manton (1964), Wyse & Dwyer (1973) and Shultz (1989). Their observations were largely confirmed in the present study (Table 1, Figs. 1–8), and another detailed description of this skeletomuscular system is not provided here. However, the literature contains persistent errors and omissions regarding muscles of the chelicerae, opercular chondrites, chilaria and preoral coxosternal apparatus. Consequently, these systems are described in greater detail here and in the following section on the preoral apparatus.

Cheliceral muscles: The chelicerae comprise three articles: protomerite, deutomerite and tritomerite (Fig. 5). Each chelicera is bordered medially by the epistome and posteriorly to laterally by the procurved epistomal horns (Fig. 4). Each chelicera is operated by four extrinsic muscles (Fig. 5), three carapace-protomerite muscles *(45–47)* that originate

from a small region on the anteromedial surface of the carapace (Fig. 1) and one endosternite-protomerite muscle (Fig. 5) that originates on the medial surface of the anterior endosternal horn. Lankester et al. (1885) were mistaken in regarding muscles *45--47* as a single muscle and in considering muscle *15* a second endosternite-protomerite muscle. The intrinsic muscles are described here for the first time. The protomerite-deutomerite joint is equipped with an extensor *(49)* and a flexor *(50)*, and the deutomerite-tritomerite joint is operated by a closer *(51)* and an opener *(52)* (Fig. 5).

Opercular chondrites and associated muscles: Muscles of the abdominal appendages have been treated in detail elsewhere (e.g., Lankester et al. 1885; Patten 1912) and these are described briefly in Table 1 and illustrated in Figs. 1 and 8. Only those associated with the opercular chondrites will be described here. Opercular chondrites are paired, roughly cylindrical structures composed of a pliable cartilaginous material (Patten & Hazen 1900; Fahrenbach 1999). Each chondrite attaches ventrally at an oval region on the anterior surface of each operculum (Fig. 8: bchdt) and projects anterodorsally, but it terminates before reaching the abdominal tergum and adheres medially to the lateral surface of the dorsal entapophysis of the same somite as the appendage from which the chondrite originates (Fig. 2C). Longitudinally adjacent chondrites interconnect dorsally through a thin horizontal sheet (Fig. 7C) composed of the same cartilaginous tissue. The shaft of each chondrite has three muscles whose fibers pass downward and attach to the anterior opercular surface near the base of the chondrite (Fig. 8: *97, 99, 100*). These muscles presumably function in compressing and/or flexing the chondrite, which may act, in turn, as an elastic and/or hydrostatic skeleton for operating the operculum.

Chilarial muscles: Xiphosurans are the only extant chelicerates to retain distinct appendages (chilaria) (Figs. 2, 4) on somite VII as adults. Each chilarium has a cartilaginous bar (chilarial chondrite) that originates near its posterior margin (Fig. 4: cht) and extends dorsally to attach to the posterior margin of the endosternite (Patten & Redenbaugh 1899: "capsuliginous bars"). This structure is composed of the same material as the opercular

Table 1.—Muscles of *Limulus polyphemus*, numbered and described. *Abbreviations:* O, origin; I, insertion; H: homologs in other studies. References to homologs consist of abbreviated author name and the reference number or name that author used in denoting the muscle. Author abbreviations: LBB, Lankester, Benham & Beck (1885); M, Manton (1964); P, Patten (1912); Sch, Scholl (1977); Sh, Shultz (1989); Sn, Snodgrass (1952).

Axial and gut muscles

1 Hundreds of loosely packed strands passing through hepatopancreas and other viscera. O: cephalothoracic carapace, dorsal surface of marginal fold. I: cephalothoracic carapace, ventral surface of marginal fold (not illustrated). H: Sch, lDvm.

2 Many long strands. O: cephalothoracic carapace, dorsal anterior surface of marginal fold. I: cephalothoracic carapace, ventral anterior surface of marginal fold (Fig. 2). Probably enlarged components of 1. H: LBB 66? (Because these muscles pass along the lateral surfaces of the crop, LBB may have mistaken these for pharyngeal muscles.)

3 Transverse, unpaired. O: base of right epistomal horn. I: base of left epistomal horn (Figs 2, 4). May be a component of 5.

4 Hundreds of short, tightly packed strands. O: abdominal tergum, dorsal surface of marginal fold. I: abdominal tergum, ventral surface of marginal fold (not illustrated).

5 Five elements (5_{II}–5_{VI}). Fibers span crests of adjacent and subadjacent intercoxal folds and epistomal horns to form preoral sphincter (Figs 2, 4).

6 O: subendosternal subneural plastron. I: anterior surface of endostoma, interdigitates with 5 (Figs 2, 4).

7 O: medial surface of endosternal horn and lateral ventral surface of endosternite. I: dorsal and dorsolateral surfaces of esophageal portion of foregut (Figs 2, 7C). H: LBB, 67; Sch, MuVd.

8 Encircles foregut, well developed around crop and gizzard (Figs 2, 7C). H: LBB, S.

9 O: postopercular sternum, anterior margin. I: rectum, ventral wall (Figs 2, 7C).

10 Sheetlike. O: tergum, posteromedial dorsal surface. I: rectum, dorsolateral surface (Figs 1, 2, 7C). Separates 36 and 37 (Fig 7B,C).

11 Nine serial groups. O: carapace and tergum, dorsal medial surfaces. I: dorsal pericardium (Fig. 1).

12 "Veno-pericardiac muscles." Nine serial members. O: ventral pericardium. I: lateral surface of endosternite (2) or ventral venous sinus (7) (Fig. 2). They span the abdominal space between muscle groups 22 and 26, and interdigitate with the members of 22. H: LBB, 68; Sch, Vpkm.

13 Six serial members, 13_I–13_{VI}. O: endosternite, dorsal surface. I: central carapace. (Figs 1, 7A). Probably serial homologs of 17. H: LBB, 49–52, 57–59; Sch, SuE 1–6.

14 O: endosternite at base of tendinous process shared with 13_{VI}. I: first dorsal entapophysis (Fig. 7A, C). May be anteriormost member of series 22 (i.e. 22_{VI}). H: LBB, 53; Sch, SuE; M: Fig. 16.

15 O: endosternal horn. I: anterior half of epistomal horn and anteriorly adjacent series of sclerites (Figs 2, 4, 9B). May be anteriormost member of series 16. H: LBB, 30 (Error: not a cheliceral muscle).

16 Three or four serial members, 16_{III}?, 16_{IV}–16_{VI}. Sheetlike. O: lateral surface of endosternite and associated marginal membrane. I: pliable cuticle between coxae of legs 1–5 (Fig. 4). See 15.

17 Seven serial members, 17_{VIII}–17_{XIV} but the "trilobite larva" has 17_{XV} (Scholl 1977: fig. 5). O: subneural plastrons (17_{VIII}–17_{XIII}) or postopercular sternum (17_{XIV}). I: tergum medial to dorsal entapophyses (Figs 1, 7C). See 13. H: LBB, 12 (errors); Sch, Dvm.

18 Thin sheet of connective tissue. O: postopercular sternum, anterior medial surface. I: tergum, medial surface posterior to 7th dorsal entapophysis (somite XIV) (Figs 1, 2).

19 Seven serial members, 19_{VII}–19_{XIII}. O: endosternite (19_{VII}) or subneural plastron (19_{VIII}–19_{XIII}). I: posteriorly adjacent subneural plastron (19_{VII}–19_{XII}) or postopercular sternum (19_{XIII}) (Figs 7C, 9B). H: LBB 5.

20 Variably expressed. O: endosternite or subneural plastron. I: subneural plastron or postopercular sternum, two or more somites posterior to origin (Figs 7C, 9B).

21 Variably expressed. O: subneural plastrons. I: dorsal entapophysis of more posterior somite. Arrangement of one individual depicted in Fig. 7C. H: LBB 13–17.

22 Seven serial members, 22_{VIII}–22_{XIV}, but the "trilobite larva" has 22_{XV} (Scholl 1977: fig. 5). O: endosternite, posterior dorsal surface. I: 1st to 7th dorsal entapophyses. Anterior-to-posterior sequence of insertions reflected in medial-to-lateral sequence of origins (Figs 7A, 9B). H: LBB, 1, 2, 54–55, 83–87, 103–107; Sch, Ent.

Table 1.—Continued.

23 Seven serial members, 23_{VIII}–23_{XIV}. O: dorsal surface of endosternite; anterior origins smaller, more medial. I: subneural plastrons of somites (23_{VIII}–23_{XIII}) and anterior margin of postopercular sternum (23_{XIV}) (Fig. 7C). H: LBB, 3 (in part).

24 Five serial members, 24_{IX}–24_{XIII}. O: medial margin of 2nd to 6th ventral entapophyses (somites IX-XIII). I: postopercular sternum, anterior margin (Fig. 7A). H: LBB, 3, 16 (in part).

25 Variable, up to four serial members. O: medial margin of 1st to 4th ventral entapophyses (somites VIII-XI); if fewer, absent posteriorly. I: 7th dorsal entapophysis (somite XIV) (Fig. 7A).

26 Seven serial members, 26_{VIII}–26_{XIV}. O: lateral margins of cardiac lobe of carapace and second dorsal entapophysis (26_{XIV} in part). I: ventral entapophyses (somites VIII-XIV) (Figs 1, 7A, B, 9B). Origin of posterior six members in quasi-concentric pattern with anteriormost element (26_{IX}) located "centrally" (Fig. 1). H: LBB, 18, 19; Sch, Btm.

27 O: carapace, cardiac lobe. I: hollow apodeme formed by invagination of hinge between carapace and tergum (Figs 1, 7B, 9B). H: LBB, 78; Sch, Dlm 7.

28 O: carapace, cardiac lobe. I: anterior margin of hinge between carapace and tergum (Figs 1, 7B, 9B). H: LBB, 78; M, "retractor dorsalis"; Sch, Dlm 7.

29 O: 1st dorsal entapophysis (somite VIII). I: hinge between carapace and tergum (Fig. 7B).

30 Four serial members, 30_{IX}–30_{XII}. O: 1st dorsal entapophysis (somite VIII). I: 2nd through 5th dorsal entapophyses (somites IX–XII) (Figs 7B, 9B). H: LBB, 4a.

Telson muscles

31 O: abdominal tergum, medial to 6th dorsal entapophysis (somite XIII). I: telson, dorsal process (Figs 1, 7B). H: LBB, 6, 120?

32 O: abdominal tergum, medial to 7th dorsal entapophysis (somite XIV). I: telson, dorsal process (Figs 1, 7B). H: LBB: 6, 101?

33 O: abdomen, 5th dorsal entapophysis (somite XII). I: telson, dorsal process (Fig. 7B). H: LBB, 93.

34 O: abdomen, 6th dorsal entapophysis (somite XIII). I: telson, dorsal process (Fig. 7B). H: LBB, 92.

35 O: abdomen, 7th dorsal entapophysis (somite XIV). I: telson, dorsal process (Fig. 7B). H: LBB, 91.

36 O: abdomen, tergum posterior to 7th dorsal entapophysis (somite XIV) medial to 37. I: telson, dorsal process (Figs 1, 7B). H: LBB, 7.

37 O: abdomen, tergum posterior to 7th dorsal entapophysis (somite XIV) lateral to 36. I: telson, dorsal process (Figs 1, 7B). H: LBB, 8.

38 O: abdomen, postopercular sternum. I: telson, dorsal process (Fig. 7B). H: LBB, 94–97.

39 O: abdomen, tergum lateral to 7th dorsal entapophysis (somite XIV). I: telson, ventrolateral process (Figs 1, 7A). Sometimes with second part originating between 36 and 37 (somite XV?).

40 O: abdomen, 5th dorsal entapophysis (somite XII). I: telson, ventrolateral process (Fig. 7A). H: LBB, 88.

41 O: abdomen, 6th dorsal entapophysis (somite XIII). I: telson, ventrolateral process (Fig. 7A). H: LBB, 89.

42 O: abdomen, 7th dorsal entapophysis (somite XIV). I: telson, ventrolateral process (Fig. 7A). H: LBB, 90.

43 O: abdomen, postopercular sternum medial to 44. I: telson, ventrolateral process (Fig. 7A). H: LBB, 10.

44 O: abdomen, postopercular sternum lateral to 43. I: telson, ventrolateral process (Fig. 7A). H: LBB, 11.

Cheliceral muscles

45 Long, thin. O: carapace, anteromedial; sometimes with additional fibers originating on endosternal horn. I: protomerite, anterior margin (Figs 1, 5). H: LBB, 24; Sch, MuCh.

46 Long, thin. O: carapace, anteromedial. I: protomerite, medial margin (Figs 1, 5). H: LBB, 24; Sch, MuCh.

47 Long, thin. O: carapace, anteromedial. I: protomerite, lateral margin (Figs 1, 5). H: LBB, 24; Sch, MuCh.

48 O: endosternal horn, medial surface. I: protomerite, posterior process (Fig. 5). H: LBB, 31.

49 O: protomerite, dorsolateral and ventroproximal surfaces. I: deutomerite, dorsal margin (Fig. 5).

50 O: protomerite, dorsomedial and ventroproximal surfaces. I: deutomerite, ventral margin (Fig. 5).

51 O: deutomerite. I: tritomerite, medial margin (Fig. 5).

52 O: deutomerite, lateral surface. I: tritomerite, lateral margin (Fig. 5).

Table 1.—Continued.

Leg muscles (legs 1–5 are appendages of somites II–VI)

53 All legs. O: carapace, near extrinsic muscles of anteriorly adjacent appendage. I: coxa, anteromedial margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 27.

54 All legs. O: carapace, near extrinsic muscles of anteriorly adjacent leg. I: coxa, anterolateral margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 26.

55 All legs. O: carapace, near extrinsic muscles of posteriorly adjacent leg. I: coxa, posteromedial margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 29.

56 All legs. O: carapace. I: coxa, posterolateral margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 28.

57 All legs. O: carapace. I: coxa, posterolateral process (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 25.

58 Leg 5. Small, thin. O: carapace, posterior. I: coxa, posterolateral (Fig. 1; see also fig. 15 in M). H: M, "dorsal coxal muscle".

59 All legs. O: endosternite, ventral surface. I: coxa, anteromedial margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 34, 37, 40, 43, 46.

60 All legs. O: endosternite, ventral surface. I: coxa, anterolateral margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 32m, 35o, 38q, 41s, 44y.

61 All legs. O: endosternite, ventral surface. I: coxa, posteromedial margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 33, 36, 39, 42, 45.

62 All legs. O: endosternite, ventral surface. I: coxa, posterolateral margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, Sn, 32n, 35p, 38r, 41t, 44z.

63 Leg 5. O: endosternite, ventral surface. I: coxa, anterior margin (not illustrated but see figs 15 and 17 in M). H: LBB, M, 47.

64 Leg 5. O: endosternite, ventral surface. I: coxa, posterior margin (not illustrated but see figs 15 and 17 in M). H: LBB, M, 60.

65 Legs 1–4. O: inner wall of preoral chamber. I: coxa, posteromedial margin with 66 in legs 2–4 and corresponding region in leg 1 (Fig. 4; see also fig. 14 in M). H: M, "sternite muscle".

66 Legs 2–4. O: coxa, posteromedial margin. I: moveable endite, anterior surface (Fig. 4; see also fig. 14 in M). H: M, "coxal endite muscle".

67 All legs. O: coxa, proximal anterior and posterior margins. I: trochanter, dorsal margin and arthrodial membrane (Fig. 6). H: Sn, 1 Leg 5. O: tarsus, ventral surface. I: apotele, ventral margin (Fig. 6). H: Sh, 2; Sn, 21.

68 All legs. O: coxa, ventral anterior surface. I: trochanter, anteroventral margin (Fig. 6). H: Sn, 2.

69 All legs: O: coxa, dorsal posterior and dorsal anterior surfaces. I: trochanter, ventral margin via heavily sclerotized tendons (Fig. 6). H: Sn, 2+3.

70 All legs. O: coxa, ventral posterior surface. I: trochanter, posteroventral margin (Fig. 6). H: Sn, 3.

71 All legs. O: dorsal arthrodial membrane of trochanter-femur joint. I: femur, proximal half with anterior, dorsal and posterior parts (71a–71c) (Fig. 6). H: Sh, 12; Sn, 7.

72 All legs. O: trochanter, posterior and ventroposterior surfaces. I: femur, posterior ventral margin (Fig. 6). H: Sh, 11; Sn, 4.

73 All legs. O: trochanter, distal anterior surface. I: femur, proximal posterior surface (Fig. 6). H: Sh, 10; Sn, 6.

74 All legs. O: trochanter, anterior and ventral surfaces. I: patellar sclerite, proximal end (Fig. 6). H: Sh, 8d; Sn, 10.

75 All legs. O: femur, middle dorsoanterior surface. I: patellar sclerite, distal shaft (Fig. 6).

76 All legs. O: femur, middle ventroposterior surface. I: patellar sclerite, distal shaft (Fig. 6). H: Sh, 8c.

77 All legs. O: femur, distal anterior surface. I: patellar sclerite, anterior arm (Fig. 6). H: Sh, 8a; Sn, 8.

78 All legs. O: femur, distal posterior surface. I: patellar sclerite, posterior arm (Fig. 6). Sh: 8b, Sn: 8.

79 All legs. O: femur, distal dorsal surface, and patella, anterior and anteroventral surfaces. I: tibia, ventral margin (Fig. 6). H: Sh, 6; Sn, 16.

80 All legs. O: femur, distal dorsal surface, and patella, posterior and posteroventral surfaces. I: tibia, ventral margin (Fig. 6). H: Sh, 7; Sn, 17.

81 All legs. O: patella, anterodorsal surface. I: tibia, anterodorsal process (Fig. 6). H: Sh, 4a; Sn, 12.

82 All legs. O: patella, posterodorsal surface. I: tibia, posterodorsal process (Fig. 6). H: Sh, 5a; Sn, 13.

83 All legs. O: patella, anterior surface. I: tibia, anterior margin (Fig. 6). H: Sh, 4b; Sn, 14.

84 All legs. O: patella, posterior surface. I: tibia, posterior proximal margin (Fig. 6). H: Sh, 5b; Sn, 15.

Table 1.—Continued.

85 Leg 5. O: tibia, anterior surface. I: tarsus, anterior margin (Fig. 6). H: Sh, 3b; Sn 18.
86 Leg 5. O: tibia, anterior and posterior surfaces. I: tarsus, posterior margin (Fig. 6). H: Sh, 3a; Sn 19.
87 All legs. Legs 1–4: O: tibiotarsus, dorsal surface (not illustrated). I: apotele, dorsal margin. Leg 5: O: tarsus, dorsal surface. I: apotele, dorsal margin (Fig. 6). H: Sh, 1; Sn, 20.
88 All legs. Legs 1–4: O: tibiotarsus. I: apotele, ventral margin (not illustrated). Leg 5: O: tarsus, ventral surface. I: apotele, ventral margin (Fig. 6). H: Sh, 2; Sn, 21.

Chilarial muscles

89 Long, thin. O: carapace, medial posterior region. I: chilarium, lateral flange (Figs 1, 4).
90 O: endosternite, posterior margin. I: chilarium, lateral flange (Fig. 4).
91 O: endosternite, posterior ventral surface near attachment of chilarial chondrite. I: chilarium, anteromedial margin (Figs 2, 4).
92 O: subendosternal subneural plastron, posterior margin. I: chilarium, medial surface (Figs 2, 4).
93 O: subendosternal subneural plastron, posterior margin. I: chilarium, lateral surface (Fig. 4).
94 Transverse. O: right chilarium at base of chondrite. I: left chilarium at base of chondrite (Figs 2, 4).

Opercular muscles

95 Genital operculum only. 0: carapace, posteromedial surface (Fig. 1). I: chondrite, dorsal surface near attachment to 1st dorsal entapophysis (not illustrated).
96 Postgenital opercula, 96_{VIII}–96_{XIII}. O: posteromedial surface of carapace (96_{VIII}) (Fig. 1) or posterior margin of dorsal entapophysis (96_{IX}–96_{XIII}). I: anterior margin of operculum of posteriorly adjacent somite near 100 (Fig. 8). H: LBB, 21, 22+23?; Sn, pmcl.
97 Opercula, 97_{VIII}–97_{XIII}. O: chondrite, anterior surface. I: operculum, anterior surface with 96 (Fig. 8).
98 Opercula, 98_{VIII}–98_{XIII}. O: tergum, near dorsal entapophysis (Figs 1, 8). I: operculum, anterior surface proximal to transverse ridge (Fig. 8). H: LBB, 20; Sn, rmcl.
99 Opercula, 99_{VIII}–99_{XIII}. O: chondrite, posteromedial surface. I. operculum, anterior surface medial to longitudinal ridge (Fig. 8).
100 Opercula, 100_{VIII}–100_{XIII}. O: dorsomedial surface of chondrite and adjacent regions of tergum; tergal part smaller posteriorly (Figs 1, 8). I: operculum, anterior surface distal and lateral to intersection of longitudinal and transverse ridges (Fig. 8). H: LBB, 20, 113.
101 Opercula, 101_{VIII}–101_{XIII}. O: carapace (101_{VIII}) (Fig. 1) or dorsal entapophysis (IX-XIII). I: anterior surface of operculum of posteriorly adjacent somite (Fig. 8). H: LBB, 21–23?
102 Opercula, 102_{VIII}–102_{XIII}. O: subneural plastron, ventral. I: chondrite, lateral face (Fig. 8). H: LBB, 48?
103 Opercula, 103_{VIII}–103_{XIII}. O: subneural plastron, ventral surface. I: basal posterior face of chondrite and/or adjacent region of operculum (Fig. 8). H: LBB, 115.
104 Opercula, 104_{VIII}–104_{XIII}. O: chondrite, posterior surface. I: exopod, medial margin of posterior plate (not illustrated).
105 Opercula, 105_{VIII}–105_{XIII}. Many separate fibers. O: anterior surface. I: posterior surface. More developed near lamellae (not illustrated).
106 Opercula, 106_{VIII}–106_{XIII}. O: operculum, medial anterior margin. I: telopod (Fig. 8). H: LBB, 114.
107 Opercula, 107_{VIII}–107_{XIII}. O: operculum, anterior surface. I: telopod base (Fig. 8). H: LBB, 112.
108 Postgenital opercula, 108_{IX}–108_{XIII}. O: telopod protopodite. I: telopod deutomerite (Fig. 8). H: LBB, 114.
109 Postgenital opercula, 109_{IX}–109_{XIII}. Telopod. O: protomerite, distal margin. I: deutomerite, proximal margin (Fig. 8).
110 Postgenital opercula, 110_{IX}–110_{XIII}. Telopod. O: deutomerite. I: tritomerite (Fig. 8).
111 Postgenital opercula, 111_{IX}–111_{XIII}. Telopod. O: deutomerite. I: tritomerite (Fig. 8).
112 Opercula, 112_{IX}–112_{XIII}. O: telopod, base. I: exopod lobe, proximal margin (Fig. 8).
113 Opercula, 113_{IX}–113_{XIII}. O: operculum, anterior surface. I: exopodial lobe, proximal margin (Fig. 8).

Figure 1.—Dorsal muscle attachments of an immature *Limulus polyphemus*. A, Cephalothoracic carapace, abdominal tergum and base of the telson. Muscles with attachments depicted in black arise from the endosternite or subneural plastrons (compare Fig. 7). B, Details of muscle attachments on the right side of the cardiac lobe of the carapace showing quasi-concentric arrangement of attachments of muscle series 26. Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral somite with which the indicated muscle or structure is associated. *Abbreviations:* af, axial furrow; de, invagination associated with dorsal entapophysis.

chondrites (Patten & Redenbaugh 1899) and is probably serially homologous with them. A transverse muscle (*94*) passes from the base of one chilarial chondrite to the base of the other (Figs. 2, 4). Each chilarium also has two muscles that originate on the subendosternal subneural plastron (*92, 93*) and two that originate on the endosternite (*90, 91*) (Figs. 2, 4). A long, thin muscle (*89*) originates on the carapace among extrinsic muscles of the append-

age of somite VI (i.e., leg 5) (Fig. 1), passes ventrally lateral to the axial muscles (*26*), and inserts on the lateral flange of the chilarium (Fig. 4).

Axial muscles.—*Endosternite:* The endosternite of *Limulus* has been described and illustrated especially well by Patten & Redenbaugh (1899) (see also Lankester et al. 1885; Pocock 1902; Snodgrass 1952; Manton 1964; Firstman 1973; Yamasaki et al. 1988) and will
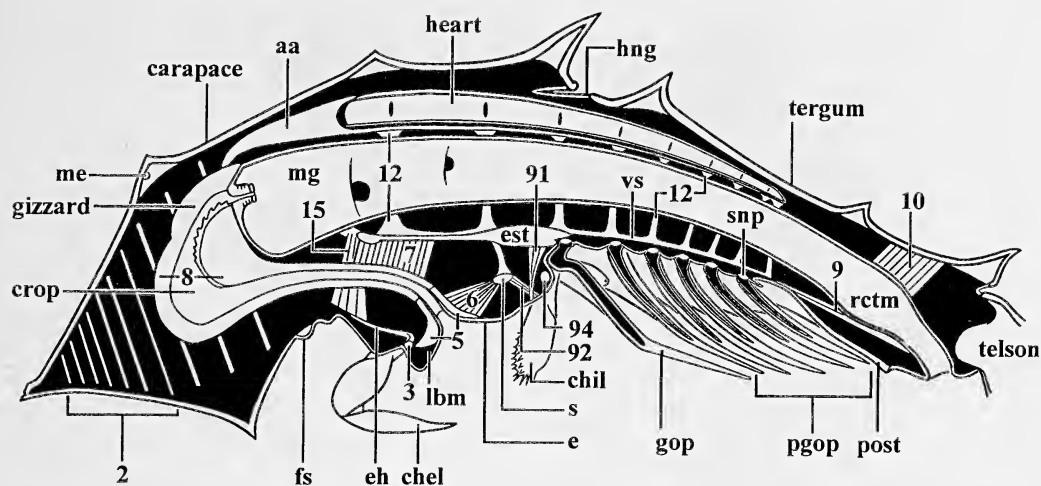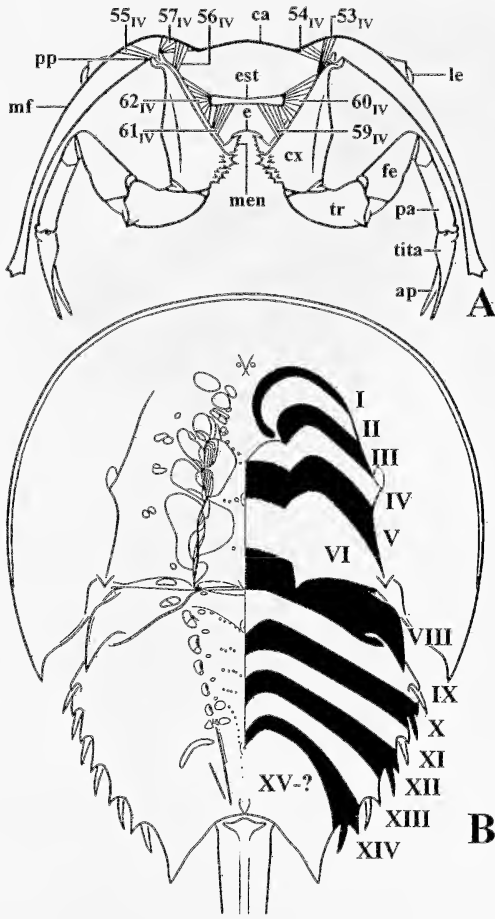
Figure 2.—Medial view of mid-sagittal section of an immature *Limulus polyphemus*. All extrinsic appendicular and axial skeletal muscles, including the endosternal suspensors, have been removed. Arabic numerals correspond to muscles listed in Table 1. *Abbreviations:* aa, anterior aorta; chel, chelicera; chil, chilarium; e, endostoma; eh, epistomal horn; est, endosternite; fs, frontal sclerite; gop, genital operculum; hng, hinge between carapace and tergum; lbm, labrum; me, medial eye; mg, midgut with openings to digestive caeca; pgop, postgenital opercula; rctm, rectum; post, postopercular sternum; s, subendosternal subneural plastron; snp, subneural plastron; vs, venous sinus (collapsed).

therefore be treated here in a general manner. The endosternite (Figs. 2, 3, 7, 9) is a mesodermally derived endoskeleton composed of a tough, fibrous connective tissue (Fahrenbach 1999). It is a roughly rectangular, horizontal sheet with a pair of anterior projections, the anterior horns (Figs. 2, 7); a pair of sheetlike posterolateral projections; and a posteromedial projection. It serves primarily as an attachment for extrinsic leg muscles (67–72) (Fig. 3A; see also Lankester et al. 1885; Manton 1964); axial muscles that attach to various sites in the abdomen (14, 19, 22, 23) (Figs. 7, 9B); pharyngeal dilator muscles (7) (Figs. 2, 7), which originate from the concave ventral surface of the endosternite; and the first two "veno-pericardiac" muscles (12) (Fig. 2). It is suspended from the carapace by six paired muscles that attach to dorsal projections which are continuous with the body of the endosternite (13) (Figs. 1, 7, 9B).

The endosternite is also connected to the body wall by a less well-understood system of ventrolateral muscles (15) and ligaments (16). The dorsal lateral margin of the endosternite is modified into a flexible marginal membrane which extends from the attachment of the first "venopericardiac" muscle (12) posteriorly to

the attachment of the second "venopericardiac" muscle (Fig. 2). Posteriorly, the membrane becomes bilayered, merges with a large lateral venous sinus and continues rearward to form the ventral sinus of the abdomen. The floor of the sinus is firmly connected to the abdominal floor and is attached dorsally to the pericardium via the seven remaining venopericardiac muscles (Fig. 2: 12). The endosternal attachment points of the first two venopericardiac muscles have membranous ligaments (16) that pass ventrolaterally from the marginal membrane to the pliable cuticle between the leg coxae. Specifically, there are two ligaments associated with the anterior "veno-pericardiac" muscle, one attaching between the appendages of somites III and IV (legs 1 and 2) and the other between appendages of somites IV and V (legs 2 and 3) (Fig. 4). The ligament associated with the posterior "venopericardiac" muscle is especially well developed and attaches between legs 3 and 4 (Fig. 4). An apparent ligament was observed extending from the lateral surface of the endosternal horn and inserting on the intercoxal cuticle between legs 1 and 2, but this was not confirmed in all individuals. Muscle 15 arises from the ventral surface of the anterior en-

Figure 3.—A, Anterior view of cross section through cephalothorax showing arrangement of extrinsic muscles of the third leg (after Wyse & Dwyer 1973). B, Dorsal view showing approximate locations of "muscular somites" composing the carapace and tergum. Note the posterior displacement of somite I (cheliceral somite) and that the lateral portions of the hinge between the carapace and tergum are specializations of somite VIII. Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral segment with which the indicated muscle is associated. *Abbreviations:* ap, apotele or moveable finger of chela; ca, carapace; cx, coxa; e, endostoma; est, endosternite; fe, femur; men, moveable endite; mf, marginal fold; le, lateral eye; pa, patella; pp, pivot point between ventral surface of marginal fold and coxa; tita, tibiotarsus; tr, trochanter.

dosternal horn and inserts on the epistomal horn that is embedded in the flexible cuticle between the chelicera and leg 1. Muscle *15* was mistaken for an extrinsic cheliceral muscle by Lankester et al. (1885).

Subneural plastrons: The subneural plastrons are metamerically arranged endoskeletal elements composed of material similar to that of the endosternite (Patten & Redenbaugh 1899). Despite apparent similarities in composition, it is unlikely that the plastrons and endosternite are serial homologs, because the endosternal element and subneural plastron of somite VII are both present (Figs. 2, 9B), and the central nervous system passes ventral to the endosternite and dorsal to the plastrons. The anteriormost subneural plastron is suspended from the ventral surface of the endosternite by processes of connective tissue (Figs. 2, 4: s) and is an attachment site for muscles of the preoral chamber and chilaria (Figs. 2, 4: *6, 92, 93*). It appears to be associated with somite VII, the chilarial somite. The remaining six subneural plastrons are located on the floor of the abdomen (Figs. 2, 7, 8: snp) and appear to belong to somites VIII to XIII (Figs. 2, 7, 9B). Each abdominal plastron spans the crests of two folds in the pliable cuticle of the ventral body wall (Fig. 2) and thereby forms a series of transverse "tunnels." Muscles (*102, 103*) arising from the opercula pass medially through these tunnels to insert on the ventral surface of the plastron (Fig. 8). A bilateral pair of connective-tissue processes project dorsally from each plastron and serves as attachment sites for a variety of axial muscles that are described in detail below.

Axial muscles of the abdomen: A notable incongruity in *Limulus* is a complex axial muscle system in the abdomen (Figs. 7, 9B), a tagma that lacks dorsal mobility between its constituent somites. The system is apparently used in flexing the dorsal hinge between the carapace and tergum during defensive "enrollment" and in moving the opercula. Lankester et al. (1885) provided a description of the axial muscle system, but it is confusing, imprecise and sometimes incorrect. The axial muscles are here categorized into four groups, 1) the dorsal longitudinal complex, 2) ventral longitudinal complex, 3) the posterior oblique complex, and 4) the anterior oblique complex.

Muscles in the dorsal longitudinal complex pass from one dorsal cuticular attachment to another. Seven muscles span the dorsal hinge between the carapace and tergum. Three paired muscles insert on the pliable fold of the dorsal hinge, two originating from the cardiac lobe of the carapace (Figs. 1, 7B: *27, 28*) and

Figure 4.—Semi-diagrammatic dorsal view of the ventral surface of the cephalothorax showing the preoral apparatus. The esophagus has been cut and reflected posteriorly to better show the arrangement of the skeletomuscular elements (compare Fig. 2). Note also that the inter-coxal bands (icb) would not normally be visible dorsally in the region of the preoral sphincter (5), because they are covered by muscle fibers that pass from each band to bands that are not directly adjacent. Note that dilator muscles (65) pass from the leg coxae and attach to the walls of the preoral chamber; their site of attachment may represent the position of the true mouth. Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral somite with which the indicated muscle or structure is associated. *Abbreviations:* a15, attachment of muscle 15; $a16_{III}$–$a16_{VI}$, attachments of 16_{III}–16_{VI}; chel, attachment site of chelicera; chf, lateral flange of chilarium; chil, chilaria; cht, base of chilarial chondrite; e, endostoma; eh, epistomal horn; fs, frontal sclerite; icb, inter-coxal band; s, subendosternal subneural plastron with tendinous attachments to the endosternite cut (compare Fig. 2).

one from the first dorsal entapophysis (Fig. 7B: *31*). The remaining four pairs originate on the posterior margin of the first dorsal entapophysis and insert sequentially on the next four pairs of dorsal entapophyses (Fig. 7B: 30_{IX}–30_{XII}).

Muscles of the ventral longitudinal complex pass from one ventral attachment to another, either a cuticular structure (ventral entapophysis, postopercular sternum) or an endoskeletal structure (endosternite or subneural plastron) (Fig. 7). The complex can be divided into three bilateral longitudinal series: a medial series, a middle series, and a lateral series. Members of the medial series are thin, strap-like muscles that originate anteriorly on one endoskeletal element and pass posteriorly to insert on another (Fig. 7C: *19, 20*). In contrast, the middle series (*23*) is best described as a collection of parallel muscle fibers with different posterior attachments. The fibers originate on the dorsal posterior surface of the endosternite and pass posteromedially to insert on the subneural plastrons and anterior margin

of the postopercular sternum, with those fibers inserting more anteriorly originating more medially on the endosternite (Fig. 7C: 23). The lateral series (24) is also composed of "fiber tracts" rather than distinct muscles. In fact, the fibers of the middle series intermingle with those of the lateral series, but the two groups can be distinguished by tracing fibers to their respective attachments. Fibers in the lateral series originate on the postopercular sternum and insert on the cuticular folds of the ventral body wall just medial to the ventral entapophyses of somites IX to XIII (Fig. 7A: 24).

Muscles of the posterior oblique complex attach dorsally to some element of the dorsal body wall (carapace, tergum, dorsal entapophysis) and ventrally to the ventral body wall or to an endoskeletal structure. This complex can also be divided into medial, middle and lateral series, and these appear to be linked morphologically to the three series of the ventral longitudinal complex. The medial series (14?, 17, 21) consists of strap-like muscles that originate on the endosternite or a subneural plastron and insert on the tergum (Figs. 1, 7C: 17) or a dorsal entapophysis (Fig. 7C: 14, 21). Members of the middle series (22) arise from the dorsal surface of the endosternite and pass dorsoposteriorly to insert on each of the dorsal entapophyses (Fig. 7A). Like the corresponding series in the ventral longitudinal complex, those muscles inserting more anteriorly originate more medially on the endosternite. The lateral series is composed of small muscles (25) that originate from the folds of the ventral body wall near the ventral entapophyses along with the fibers of the lateral series of the ventral longitudinal complex (Fig. 7A).

Muscles of the anterior oblique complex (26_{VIII}–26_{XIV}) originate on the carapace at the extreme lateral portion of the cardiac lobe (Fig. 1), and, in one case (26_{XIV}), on the second dorsal entapophysis (Fig. 7C). The first member of this complex (26_{VIII} is a small, thin muscle that inserts on a small infolding, or ventral entapophysis, on the ventral body wall at the attachment of the posterior margin of the endosternite with pliable ventral cuticle anterior to the genital operculum (Fig. 7A: ve_{VIII}). The remaining muscles originate in a quasi-concentric pattern, with those having a more anterior insertion originating nearer to the center of the origin and muscles with more posterior insertions originating more peripherally (Fig. 1). These muscles insert at the ends of long, hollow tendons which are extensions of infoldings (ventral entapophyses) of the pliable cuticle between adjacent opercula (Fig. 7).

Feeding apparatus.—The basic anatomy of the gnathobasic feeding apparatus and digestive tract of *Limulus* and other xiphosurans is well known and has been described in considerable detail by previous workers (Lankester et al. 1885; Manton 1964; Wyse & Dwyer 1973; Clarke 1979; Yamasaki et al. 1988; Fahrenbach 1999; etc.). Consequently, muscles associated with the feeding and digestive systems have been listed and briefly described in Table 1 but are not described in detail here. However, several features of the anterior digestive tract have been overlooked or inadequately described by previous workers, and these are treated in more detail.

Preoral apparatus: The preoral chamber is shaped like an inverted funnel (Figs. 2, 4) surrounded by the leg coxae (Figs. 3, 4). Its walls are formed by lobes of pliable cuticle, with the moveable and fixed endites of the leg coxae projecting between them (see Manton 1964: figs. 14, 16). The furrows between the lobes are continuous laterally with those formed by the flexible inter-coxal cuticle. The anterior wall of the chamber is an unpaired lobe that is continuous with the labrum and epistome (Fig. 2), and the posterior wall consists of an oblong plate, the endostoma, composed of stiffer but still flexible cuticle (Figs. 2–4). The chamber narrows as it passes deeper into the body and bends anteriorly to pass through the brain and to become the 'esophageal' region of the foregut (Fig. 2). There is no gross cuticular feature demarcating the "true mouth," that is, the junction of the preoral chamber and foregut.

The musculature of the preoral chamber is described in detail here for the first time. The inner surface of the walls of the preoral chamber are surrounded by a roughly circular meshwork of muscle fibers (5) that forms a large sphincter (Figs. 2, 4). The sphincter has a radially arranged 'skeleton' formed by strips of connective tissue that begin laterally on the pliable inter-coxal cuticle medially adjacent to the attachments of the endosternite-intercoxal muscles (21) and pass centripedally along the ventral body surface onto the walls of the

preoral chamber (Fig. 5). These bands occupy the internal crests of the inter-coxal folds between the lobes of the preoral chamber and may act to maintain the shape of the preoral chamber. Muscle fibers (5) arise from each cartilage-like band and associated cuticle and pass to adjacent and subadjacent bands. It is noteworthy that the inter-coxal portion of the anteriormost pair of bands appears to have been modified, or replaced, by the epistomal horns, which pass between the chelicerae and the coxae of the first leg pair (Figs. 2, 4). In fact, like the connective tissue bands, each epistomal horn is associated with a muscle (20) that arises from the endosternite (Figs. 2, 4). The epistomal horns wrap around the posterior margin of the chelicerae and join the body of the epistome, whereupon the sclerite assumes the appearance of a connective tissue band, gives rise to muscle fibers (5), and defines the lateral margins of the labrum or anterior lobe of the complex (Fig. 4). Apparent dilator muscles (73) arise from the postero-medial coxal margins of legs 1–4 and pass centripedally to insert in a ring around the deeper, narrower region of the preoral chamber (Fig. 4). The attachment of these muscles separates the roughly circular fibers of the preoral sphincter from those of the foregut (8) (Figs. 2, 3) and may indicate the site of the true mouth.

Foregut: The foregut is the cuticle-lined region of the digestive tract that connects the preoral chamber and midgut (Figs. 2C, 3). The foregut is essentially C-shaped in lateral perspective (Fig. 2). The narrow "esophageal" portion of the foregut passes anteriorly through the brain. The longitudinally folded lumen is surrounded by circular constrictor muscles (8) and is supplied with one well-developed dilator muscle arising from the endosternite (Figs. 2, 7: 7). A second dilator described and illustrated by Lankester et al. (1885) was never observed and was probably based on a misinterpretation of dorsoventral muscles that arise form the anteroventral surface of the cephalothorax, pass dorsally along the lateral surfaces of the crop, but continue dorsally to insert on the carapace (Fig. 2: 2). The foregut then expands, both in the diameter of the lumen and thickness of circular muscles, and turns dorsally and then posteriorly (Figs. 2, 5C). The lumen walls become progressively more heavily sclerotized as the foregut approaches the midgut, and the last portion (proventriculus or gizzard) is apparently specialized for grinding. The foregut is separated from the midgut by a strongly developed valve (Fig. 2).

DISCUSSION

Evolutionary morphology of axial muscles in Chelicerata.—*The box-truss axial muscle system:* Comparative anatomical studies of crustaceans (e.g., Cephalocarida, Malacostraca, Mystacocarida, Branchiopoda: Hessler 1964), myriapods (e.g., Pauropoda: Verhoeff 1934, Tiegs 1947), hexapods (Diplura: Manton 1972; Microcoryphia: Birket-Smith 1974) and, perhaps, trilobites (Cisne 1981) have revealed a common box-truss axial muscle system (Fig. 9A). This system consists of bilateral dorsal and ventral longitudinal elements that attach to each somite, a bilateral set of dorsoventral muscles within each somite that passes from the tergite to the ventral body wall, a bilateral set of posterior oblique elements that arises ventrally in association with dorsoventral elements and inserts dorsally on a more posterior somite, and a bilateral pair of anterior oblique elements that also arises ventrally with a dorsoventral elements but inserts dorsally on a more anterior somite. The ventral longitudinal, dorsoventral, anterior oblique and posterior oblique elements all attach to a transverse endoskeletal bar within each somite (Fig. 9A). Axial muscles of arachnids appear to correspond to elements of the box-truss system (Fig. 9C); that is, the dorsal longitudinal muscles and endosternite plus ventral longitudinal muscles correspond to the dorsal longitudinal and ventral longitudinal elements, respectively; dorsal endosternal suspensors and dorsoventral muscles of the opisthosoma appear to correspond to the dorsoventral elements; and the dorso-posterior endosternal suspensors and, perhaps, "transverse" muscles of the opisthosoma (e.g., Amblypygi: Shultz 1999: muscle 22; Araneae: Whitehead & Rempel 1959: muscle 89; Scorpiones: original observation) can be homologized with posterior oblique elements. No muscles corresponding to the anterior oblique elements are known in arachnids (Fig. 9C). However, it is unclear from these comparisons whether the relative simplicity of arachnids is a primitive antecedent of the box-
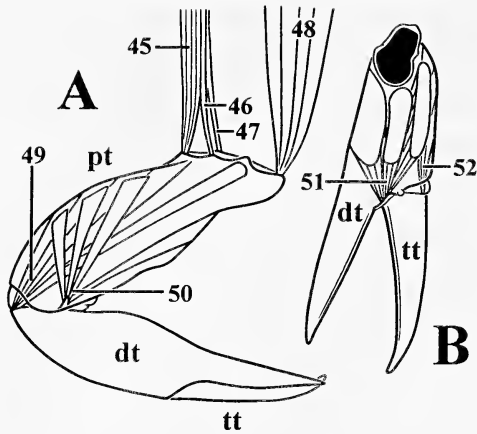
Figure 5.—Skeletomuscular anatomy of the chelicerae. A, Medial view of the right chelicera showing insertions of extrinsic muscles (45–48) and proximal intrinsic muscles (49, 50). B, Distal articles of the right chelicera showing intrinsic muscles that operate the chela (51, 52). The figure shows a dorsal view of a fully flexed chelicera. Numbers correspond to muscles listed in Table 1. *Abbreviations:* pt, protomerite or first cheliceral article; dt, deutomerite or second cheliceral article; tt, tritomerite or third cheliceral article.

truss system or a derived reduction of the box-truss system.

Based on information obtained in the present study, I propose that the abdominal axial muscle system in *Limulus* retains all essential components of the box-truss system, including the anterior oblique elements (Fig. 9B), and that the box-truss system is the plesiomorphic condition in Chelicerata. Specifically, the dorsal longitudinal elements of the box-truss system are retained as muscles *27–30* and perhaps *31–35* (Fig. 7); the ventral longitudinal elements are retained as muscles *19, 20, 23* and *24* (Fig. 7); the dorsoventral elements are retained as muscles *13* and *17* (Fig. 7); the posterior oblique muscles are retained as muscles *21, 22* and perhaps *25*; and the anterior oblique muscles are retained as muscle series *26*. Most of these comparisons are probably non-controversial, except for the anterior oblique muscles (*26*). Specifically, all relevant muscles in *Limulus* other than *26* are already accepted as axial muscles, and the necessary evolutionary transformation of a portion of the posterior oblique elements into muscle series *22* (i.e., anterior migration of the ventral attachments from each abdominal somite to

the dorsal surface of the endosternite) has been documented in ontogeny (see Scholl 1977: Figs. 3, 5). However, muscle series *26* is generally considered a group of extrinsic opercular muscles, not axial muscles, and this inconsistency must be addressed.

Lankester et al. (1885) and many subsequent authors have referred to muscle series *26* as "branchio-thoracic" muscles and considered them to be extrinsic opercular muscles, although the anteriormost member of this series (26_{VIII}) was recognized for the first time in the present study. My conclusion that these are actually axial muscles is based on the following lines of evidence: 1) One muscle (26_{XIV}) is associated with a somite that lacks appendages during all stages of development (Scholl 1977). 2) The ventral entapophyses, which give rise to the long tendons on which these muscles insert, are invaginations of the body wall rather than the appendages. This is particularly evident in the ventral entapophysis associated with 26_{XIV} which is continuous with the postopercular sternum (Fig. 7). 3) The bases of the ventral entapophyses and the adjacent region of the abdominal floor serve as attachment sites for muscles that are clearly axial rather than appendicular in origin (Fig. 7: *24, 25*). 4) The muscles insert on the cardiac lobe medial to the axial furrow, not lateral to the furrow like all appendicular muscles (Fig. 1: *53–57*), including those associated with the genital operculum (Fig. 1: 96_{VIII}, 101_{VIII}). I suggest that members of muscle series *26* may have been misinterpreted as extrinsic opercular muscles due to the erroneous assumption that the postgenital opercula are formed by medial fusion of the paired appendages, an evolutionary process that would be expected to obliterate the ventral body wall between them and its associated axial muscles. In fact, however, the abdominal floor is present externally between each postgenital operculum as a triangular fold (e.g., Snodrass 1952) and internally serves as an attachment site for the unambiguous axial muscles described above.

Given these arguments, I hypothesize that *Limulus* retains the abdominal elements of a box-truss system like that observed in other arthropod groups, although certain elements have been modified (Fig. 9). The principal evolutionary transformations required by this hypothesis are anterior migrations of portions
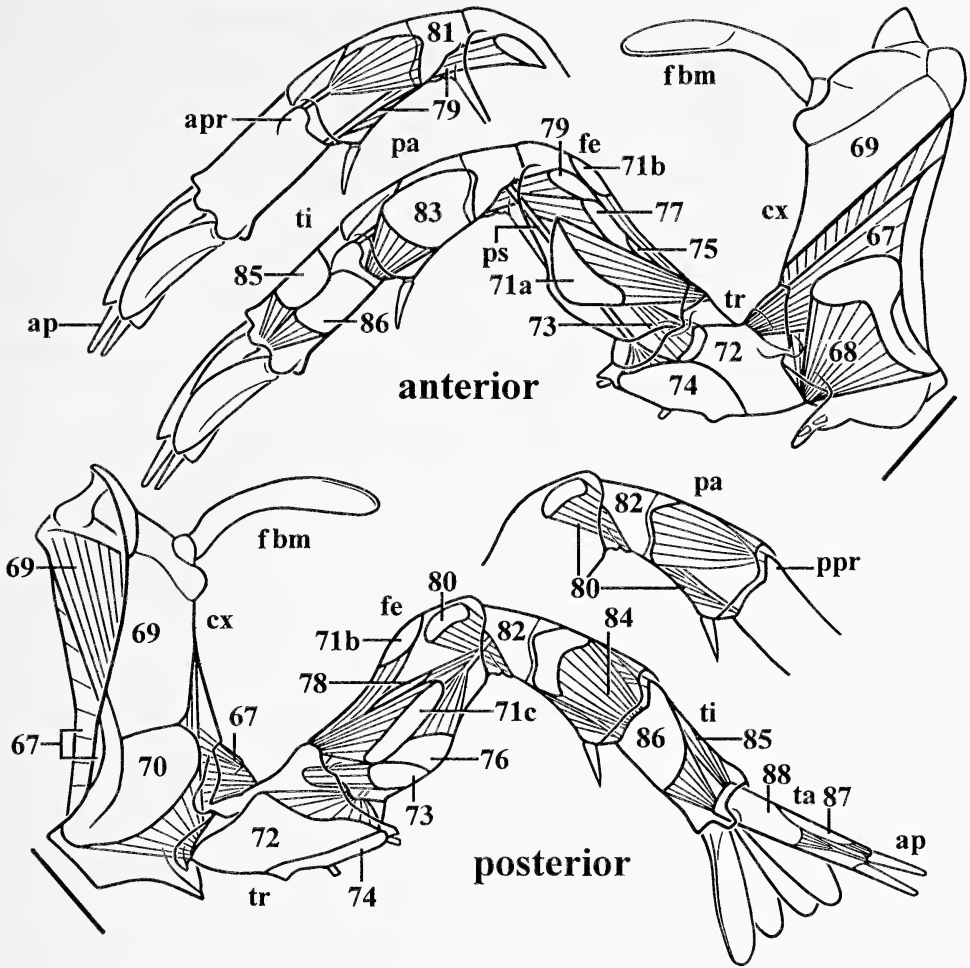
Figure 6.—Muscular anatomy of the intrinsic muscles of leg 5 from anterior and posterior perspectives. Insets show deeper muscles with superficial muscles removed. The lines near the coxae indicate the mid-sagittal plane of the intact animal. *Abbreviations:* ap, apotele; apr, anterior process of tibia; cx, coxa; fbm, flabellum; fe, femur; pa, patella; ppr, posterior process of tibia; ps, patellar sclerite; ta, tarsus; ti, tibia; tr, trochanter.

of the ventral attachments of the posterior oblique elements to the dorsal surface of the endosternite and anterior migration of the dorsal attachments of the anterior oblique elements to the carapace. These transformations would likely be associated with the evolutionary elimination of all tergal articulations except the carapace-tergum hinge (summarized by Anderson & Selden 1997), as they would allow the muscles to retain a function in moving the body. If this scenario is correct, the box-truss axial muscle system should probably be regarded as synapomorphic for Arthropoda and plesiomorphic for Chelicerata (Edgecombe et al. 2000), and the losses re-

sulting in simplification of the box-truss system, especially the loss of all anterior oblique elements, would be synapomorphic for Arachnida.

Endosternal evolution in Chelicerata: Firstman (1973) proposed a primitive axial muscle system for Chelicerata that was remarkably similar to the box-truss model. He hypothesized that the primitive system was ladderlike with a "rung" of connective tissue (transverse endoskeletal bar) positioned transversely within each somite and connected to longitudinally adjacent transverse bars by ventral longitudinal muscles. Each transverse bar was also suspended from the exoskeleton by bilat-
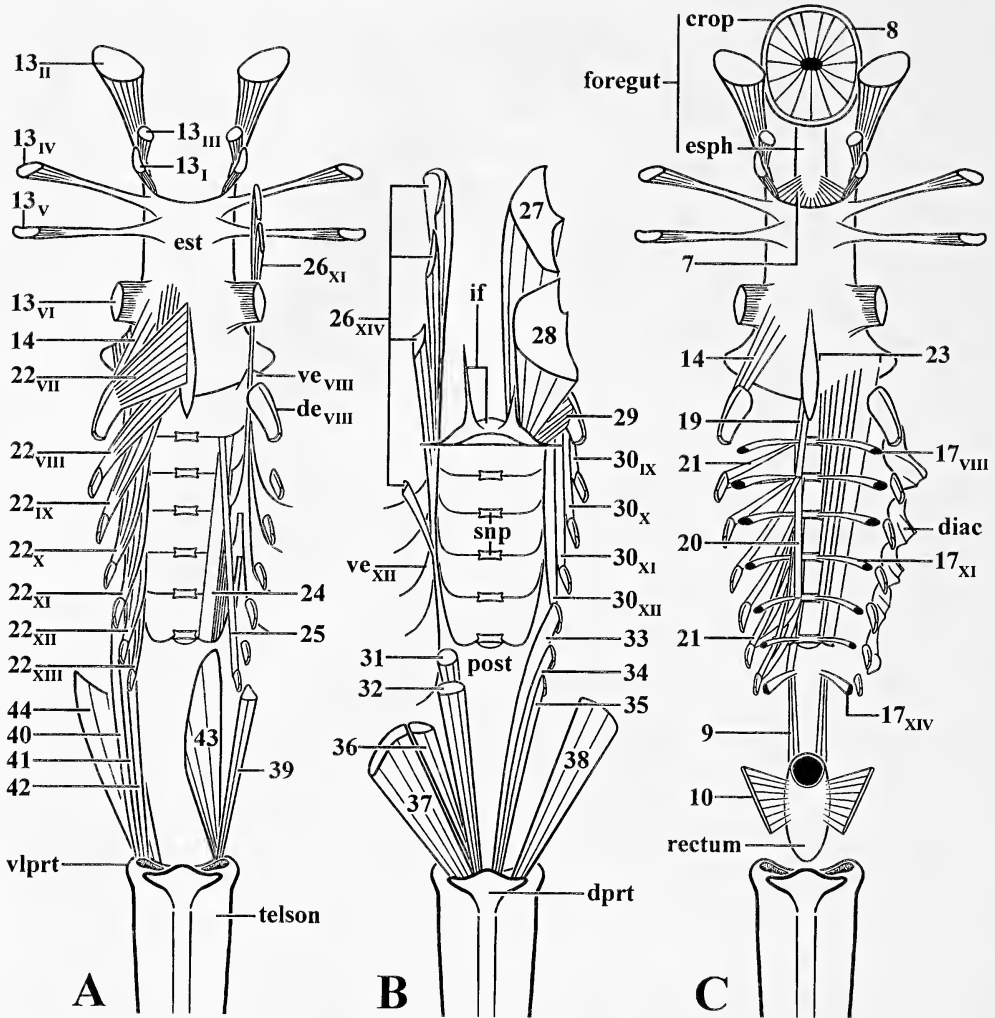
Figure 7.—Dorsal view of the endosternite (est), ventral surface of the abdomen, and the base of the telson. The appendages, carapace, tergum and most other heavily sclerotized structures have been removed, but the dorsal entapophyses (de) have been cut at their attachments to the tergum and are depicted as "floating" at their intact anatomical positions. The ventromedial surface of the abdomen is composed of pliable cuticle arranged in transverse folds. A series of subneural plastrons (snp) bridge the crests of a pair of adjacent folds (compare Fig. 2). A, The left side shows the middle tract of the posterior oblique muscles (22). The right side shows the lateral tract of ventral longitudinal muscles (24) and posterior oblique muscles (25). Only one member of the anterior oblique tract (26_{XI}) is shown, the others have been cut near their ventral attachments. The posterior end shows the arrangement of muscles that insert on the ventrolateral processes of the telson (39–44). B, Same perspective as in A, but the medial invaginated portion of the carapace-tergum hinge (if) "floats" above the other elements to show the attachments of muscles 27–29. The left side shows the arrangement of the posteriormost anterior oblique muscle (26_{XIV}), the right side shows muscles that span the dorsal entapophyses (30), and the posterior end shows the arrangement of muscles that insert on the dorsal process of the telson (31–38). C, Same perspective showing the position of the gut and its muscles (7–10). The crop and rectum have been cut horizontally and the intermediate portions of the gut have been removed to show the underlying endoskeleton and muscles (compare Fig. 2). The right side depicts the dorsoventral muscles (17) and the medial tracts of ventral longitudinal muscles (19, 20) and posterior oblique muscles (21). The left side shows the middle tract of ventral longitudinal muscles (23) and the dorsal interconnections between opercular chondrites (diac). Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral somite with which the indicated muscle or structure is associated. *Abbreviations:* de, dorsal

eral dorsoventral suspensor muscles and from the lateral exoskeleton by transverse suspensor muscles. As in the box-truss model, the endosternite would have evolved by fusion of the transverse bars and the tendinified longitudinal muscles of the first seven postoral somites. Thus, Firstman's model departed from the box-truss model only in predicting a series of intra-segmental transverse muscles in chelicerates rather than intersegmental posterior oblique muscles and, apparently, in regarding the "branchio-thoracic" muscles (*26*) as extrinsic appendicular muscles rather than axial muscles.

Upon applying his model to the axial system in *Limulus*, Firstman (1973) concluded that the endosternite retained six pairs of endosternal suspensor muscles, namely, the dorsal, transverse and ventral suspensors of somites III, the dorsal and transverse suspensors of somite IV, and the dorsal suspensors of somite V. However, observations from the present study are not consistent with Firstman's (1973) interpretation. First, he overlooked or omitted several endosternal and axial muscles in *Limulus*, specifically, one dorsal suspensor (*13*$_I$) (Figs. 1, 7), all axial muscles that arise from the endosternite and insert on more posterior structures (Fig. 7: *14, 19, 20, 22–24*), and the anterior oblique muscles (*26*) (Figs. 1, 7). Second, Firstman implied in his figures that transverse suspensors were present in the abdominal somites of *Limulus*, although he recognized in the text that these muscles (probably *102* and *103*: Fig. 8) inserted on the opercula rather than the lateral body wall and doubted their homology with the transverse suspensors of the endosternite. Third, he did not provide specific criteria for assigning muscles to particular somites (e.g., position with respect to other muscles). Fourth, he appeared to assign suspensor muscles to the "dorsal" and "transverse" series based on whether the muscle had a dorsoventral or transverse orientation rather than some more precise criterion, such as placement with respect to other muscles that could be assigned unambiguously to specific somites. [Recent studies of
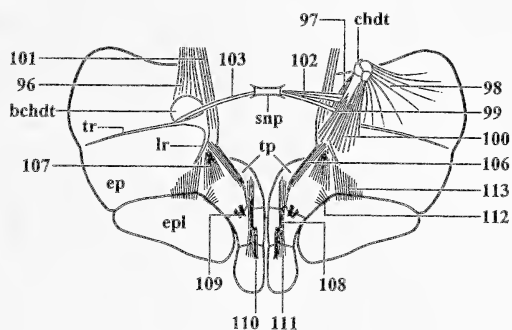
Figure 8.—Dorsal view of the first postgenital operculum with the posterior surfaces and respiratory lamellae removed. The appendage is shown in its fully retracted position, so the inner surface of the anterior surface faces dorsally. The subneural plastron (snp) of somite VIII is the only other structure depicted; the pliable ventral cuticle in which the opercula are embedded has been removed. The anatomical relationship between the appendage and the other abdominal structures can be envisioned by superimposing this figure on appropriate elements of Fig. 7. Numbers correspond to muscles listed in Table 1. *Abbreviations:* bchdt, site where the base of the appendicular chondrite attaches to the anterior plate; chdt, dorsal terminus and shaft of chondrite; ep, inner surface of the anterior plate; epl, exopodial lobe; lr, longitudinal ridge; snp, subneural plastron of somite IX; tp, telopod; tr, transverse ridge.

arachnid anatomy suggest that muscles Firstman homologized as "transverse suspensor muscles" represent different kinds of muscles in different chelicerate taxa, such as ventral suspensors in scorpions (pers. obs.) and posterior oblique muscles in Pedipalpi (Shultz 1993, 1999)].

In contrast, current evidence from *Limulus* suggests that the endosternal suspensors acknowledged by Firstman are members of a single metameric series representing somites II through VI. This is consistent with embryological evidence (Scholl 1977) and with the pattern of suspensor insertions on the carapace, which shows one suspensor associated with each set of extrinsic appendicular muscles (Fig. 1: *13*$_{II}$–*13*$_{VI}$). Firstman apparently overlooked one dorsal suspensor muscle that

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appendicular chondrites; dprt, dorsal process of telson; esph, esophageal portion of foregut; est, endosternite; if, intersegmental fold of carapace-tergum hinge; post, postopercular sternum; snp, subneural plastron; ve, ventral entapophysis; vlprt, ventrolateral process of telson.
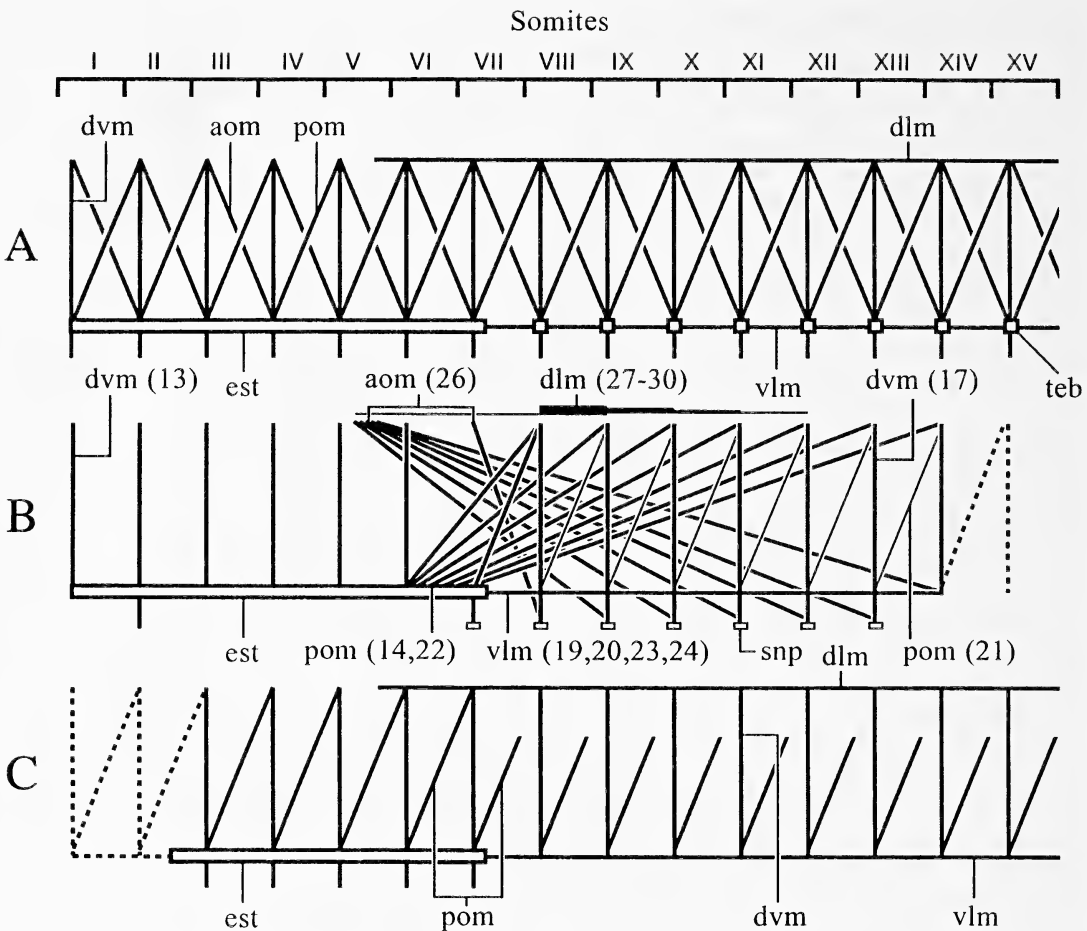
Figure 9.—Diagrammatic medial views of hypothetical axial muscle systems in chelicerates showing how the box-truss axial muscle system of other arthropods may have been modified in *Limulus* and arachnids. A, Hypothetical ancestral chelicerate condition showing primitive box-truss axial-muscle system and the chelicerate endosternite. B, Arrangement of axial muscles in *Limulus* labeled to show proposed homologies with the box-truss axial-muscle system in "A." Note simplification of prosomal elements and anterior displacement of dorsal attachments of aom and ventral attachments of pom. The dotted lines at the posterior indicate muscles present in the larva but not in adult. C, Hypothetical ancestral arachnid condition showing loss or modification of anterior elements, loss of aom in all somites, and displacement of opisthosomal pom attachments from tergites to pleural regions. Abbreviations: aom, anterior oblique muscle; dvm, dorsoventral muscle; est, endosternite; pom, posterior oblique muscle; teb, transverse endoskeletal bar; vlm, ventral longitudinal muscle.

appears to be associated with the cheliceral somite (Figs. 1, 7: 13_I). This muscle arises and inserts more posteriorly than would be expected from its metameric position due to posterior migration of the entire cheliceral somite during development (Scholl 1977) (Fig. 3). With the recognition of 13_I, *Limulus* appears to have a single metameric series of six dorsal endosternal suspensors (13_I–13_VI), one for each of the six original prosomal somites.

When these conclusions are interpreted in

the framework of the box-truss model, several evolutionary and phylogenetically relevant insights emerge. First, anterior oblique muscles are absent from the endosternite in both xiphosurans and arachnids, and this might represent a synapomorphy for these two lineages. However, given the extreme reduction of all axial muscles in pycnogonids (Firstman 1973), it is possible that this feature is synapomorphic for Chelicerata. Second, posterior oblique muscles are absent from the first five

somites of the endosternite in *Limulus* but are present for somites III-V in at least some arachnids (i.e., Araneae, Amblypygi, Thelyphonida) (Shultz 1991, 1993, 1999). Thus absence of posterior oblique endosternal suspensors in *Limulus* and all Asian species of horseshoe crabs (Yamasaki et al. 1988) is probably a synapomorphy of extant Xiphosura. Third, the apparent absence of endosternal components associated with somites I and II is a possible synapomorphy of Arachnida, given that they are present in *Limulus*. It should be noted, however, that these endosternal components may have been retained but modified and incorporated into the epipharyngeal complex of arachnids in a variety of ways (Shultz 1993, 2000). Fourth, the presence of a postcerebral pharynx supplied with dilator muscles that arise from the endosternite may be a plesiomorphic condition for Arachnida rather than a derived feature of Araneae and Amblypygi alone as is widely thought (e.g., Wheeler & Hayashi 1998). A muscularized postcerebral pharynx is clearly present in *Limulus* (Figs. 2, 7C) and has been reported but not confirmed in a palpigrade by Rucker (1901). An unmuscularized postcerebral pharynx (cuticle-lined "esophagus" only) and endosternal foramen instead of pharyngeal dilator muscles are present in Uropygi (Millot 1949; Shultz 1993).

Monophyly of Arachnida.—The vast majority of phylogenetic analyses of Chelicerata have concluded that Xiphosura and Arachnida are sister groups among extant chelicerates and that each group is monophyletic. This conclusion is strongly and consistently supported by phylogenetic analyses of morphological evidence (Weygoldt & Paulus 1979; Shultz 1990; Edgecombe et al. 2000), molecular evidence (Regier & Shultz 1997, 1998; Shultz & Regier 2000; but see Colgan et al. 1998; Giribet & Ribera 2000) and combined evidence (Wheeler & Hayashi 1998; but see Edgecombe et al. 2000). Morphological synapomorphies supporting the monophyly of Arachnida include 1) reduced pleural fold (doublure) in the prosomal carapace (Shultz 1990); 2) slit sensilla (Weygoldt & Paulus 1979; Shultz 1990); 3) anterodorsal rotation of anterior prosoma resulting in anteroventrally directed mouth (Weygoldt 1979); 4) absence of appendages on somite VII in adults (Shultz 1990); 5) absence of cardiac lobe or glabella on carapace (original observation); 6) single medial genital opening rather than bilaterally paired genital openings (paired genital openings in all extant xiphosurans: Yamasaki et al. 1988; single median opening in arachnids: Clarke 1979, original observations); 7) absence of appendages on somite XIII (Shultz 1990; but see Dunlop 1998); 8) loss or reduction of postcerebral crop and proventriculus (present study); 9) absence of anterior oblique axial muscles (present study); 10) pleural rather than tergal attachments of opisthosomal posterior oblique axial muscles (present study); and 11) endosternal suspensors of somites I and II absent or detached from the endosternite (present study). However, alternative phylogenetic systems have been proposed. Van der Hammen (1985, 1989) suggested that Xiphosura, Scorpiones and Opiliones be placed within a clade (Myliosomata) based on presence of a "coxisternal" feeding apparatus, a feature that actually appears to be primitive for all extant arthropods, including myriapods and hexapods (Popadic et al. 1998; Scholtz, Mittmann & Gerberding 1998). Dunlop (1998) suggested that scorpions are more closely related to xiphosurans than to tetrapulmonate arachnids (Araneae, Amblypygi, Uropygi), because the tetrapulmonates retain primitive lamellate respiratory structures on the genital somite but scorpions and xiphosurans have lost them (see Weygoldt 1998 for an alternative view). Each dissenting view is derived from interpretation of a single character system and the devaluation or dismissal of all characters that do not support its conclusions. Given the explicit enumeration of arachnid synapomorphies offered here and elsewhere, workers who maintain that xiphosurans be placed among arachnids should provide explicit justification for their position and specific reasons for rejecting the accumulating evidence that excludes xiphosurans from Arachnida.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, L.I. & P.A. Selden. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. Lethaia 30:19–31.

Bonaventura, J., C. Bonaventura & S. Tesh, eds. 1982. Physiology and Biology of Horseshoe Crabs: Studies on Normal and Environmentally Stressed Crabs. A.R. Liss, New York.

Birkett-Smith, S.J.R. 1974. On the abdominal morphology of Thysanura (Archaeognata and Thysanura s. str.). Entomologica Scandinavica Supplement 6:1–67.

Cisne, J.L. 1981. *Triarthrus eatoni* (Trilobita): Anatomy of its exoskeletal, skeletomuscular, and digestive systems. Palaeontographica Americana 9(53):1–142.

Clarke, K.U. 1979. Visceral anatomy and arthropod phylogeny. Pp. 467–549. *In* Arthropod Phylogeny. (A.P. Gupta, ed.). Van Nostrand Reinhold, New York.

Cohen, E., (ed.) 1979. Biomedical Application of the Horseshoe Crab (Limulidae). A.R. Liss, New York.

Colgan, D.J., A. McLauchlan, G.D.F. Wilson, S.P. Livingston, G.D. Edgecombe, J. Macaranas, G. Cassis & M.R. Gray. 1998. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Australian Journal of Zoology 46:419–437.

Damen, W.G.M., M. Hausdorf, E-A. Seyfarth & D. Tautz. 1998. A conserved mode of head segmentation in arthropods revealed by the expression pattern of Hox genes in a spider. Proceedings of the National Academy of Sciences USA 95:10665–10670.

Dunlop, J.A. 1998. The origins of tetrapulmonate book lungs and their significance for chelicerate phylogeny. Pp. 9–16. *In* Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. (P.A. Selden, ed.). British Arachnological Society, Burnham Beeches, Buckinghamshire, England.

Edgecombe, G.D., G.D.F. Wilson, D.J. Colgan, M.R. Gray & G. Cassis. 2000. Arthropod cladistics: Combined analysis of histone H3 and U2 snRNA sequences and morphology. Cladistics 16:155-203.

Fage, L. 1949. Classe des Mérostomacés. Pp. 219–262. *In* Traité de Zoologie, Vol. 6. (P.-P. Grassé, ed.). Masson, Paris.

Fahrenbach, W.H. 1999. Merostomata. Pp. 21–115. *In* Microscopic Anatomy of Invertebrates, Vol. 8A. Chelicerate Arthropoda. (F.W. Harrison & R.F. Foelix, eds.). Wiley-Liss, New York.

Firstman, B. 1973. The relationship of the chelicerate arterial system to the evolution of the endosternite. Journal of Arachnology 1:1–54.

Giribet, G. & C. Ribera. 2000. A review of arthropod phylogeny: New data based on ribosomal DNA sequences and direct character optimization. Cladistics 16:204–231.

Hammen, L. van der. 1985. Functional morphology and affinities of extant Chelicerata in evolutionary perspective. Transactions of the Royal Society of Edinburgh: Earth Sciences 76:137–146.

Hammen, L. van der. 1989. An Introduction to Comparative Arachnology. SPB Academic Publishing, The Hague.

Hessler, R.R. 1964. The Cephalocarida: Comparative skeletomusculature. Memoirs of the Connecticut Academy of Arts & Sciences 16:1–97.

Iwanoff, P.P. 1933. Die embryonale Entwicklung von *Limulus moluccanus*. Zoologische Jahrbücher Anatomie 56:163–348.

Lankester, E.R. 1881. *Limulus* an arachnid. Quarterly Journal of Microscopical Science, New Series 21:504–548, 609–649.

Lankester, E.R. 1885. A new hypothesis as to the relationship of the lung-book of *Scorpio* to the gill-book of *Limulus*. Quarterly Journal of Microscopical Science 25:339–342.

Lankester, E.R., W.B.S. Benham & E.J. Beck. 1885. On the muscular and endoskeletal systems of *Limulus* and *Scorpio*; with some notes on the anatomy and generic characters of scorpions. Transactions of the Zoological Society of London 11:311–384.

Manton, S.M. 1964. Mandibular mechanisms and the evolution of arthropods. Philosophical Transactions of the Royal Society of London B 7(737):1–183.

Manton, S.M. 1972. The evolution of arthropodan locomotory mechanisms. Part 10. Locomotory habits, morphology and evolution of the hexapod classes. Journal of the Linnean Society (Zoology) 51:203–400.

Millot, J. 1949. Ordre des Uropyges. Pp. 533–562. *In* Traité de Zoologie, Vol. 6. (P.P. Grassé, ed.). Masson, Paris.

Milne-Edwards, A. 1873. Recherches sur l'anatomie des Limules. Annales des Sciences Naturelles. Zoologie, 5th Series 17:1–67.

Owen, R. 1873. On the anatomy of the American king crab (*Limulus polyphemus* Latr.). Transactions of the Linnean Society of London 28:459–506.

Patten, W. 1893. On the morphology and physiology of the brain and sense organs of *Limulus*. Quarterly Journal of Microscopical Science 35:1–96.

Patten, W. 1912. The Evolution of the Vertebrates and their Kin. P. Blakiston's Son and Co., Philadelphia.

Patten, W. & A.P. Hazen. 1900. The development of the coxal gland, branchial cartilages, and genital ducts of *Limulus polyphemus*. Journal of Morphology 16:459–490.

Patten, W. & W.A. Redenbaugh. 1889–1900. Studies on *Limulus*. Journal of Morphology 16:1–26, 91–200.

Pocock, R.I. 1902. Studies on the arachnid endos-

ternite. Quarterly Journal of Microscopical Science 46:225–262.

Popadić, A., G. Panganiban, D. Rusch, W.A. Shear & T.C. Kaufman. 1998. Molecular evidence for the gnathobasic derivation of arthropod mandibles and for the appendicular origin of the labrum and other structures. Development Genes and Evolution 208:142–150.

Regier, J.C. & J.W. Shultz. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. Molecular Biology and Evolution 14:902–913.

Regier, J.C. & J.W. Shultz. 1998. Molecular phylogeny of arthropods and the significance of the Cambrian "explosion" for molecular systematics. American Zoologist 38:918–928.

Rucker, A. 1901. The Texan *Koenenia*. American Naturalist 35:615–630.

Scholl, G. 1977. Beiträge zur Embryonalentwicklung von *Limulus polyphemus* L. (Chelicerata, Xiphosura). Zoomorphologie 86:99–154.

Scholtz, G., B. Mittmann & M. Gerberding. 1998. The pattern of *Distal-less* expression in the mouthparts of crustaceans, myriapods and insects: New evidence for a gnathobasic mandible and the common origin of Mandibulata. International Journal of Developmental Biology 42: 801–810.

Sekiguchi, K. (ed.) 1988. Biology of Horseshoe Crabs. Science House Co., Tokyo.

Shultz, J.W. 1989. Morphology of locomotor appendages in Arachnida: Evolutionary trends and phylogenetic implications. Zoological Journal of the Linnean Society 97:1–56.

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6:1–38.

Shultz, J.W. 1993. Muscular anatomy of the giant whipscorpion, *Mastigoproctus giganteus* (Arachnida, Uropygi), and its evolutionary significance. Zoological Journal of the Linnean Society 108: 335–365.

Shultz, J.W. 1999. Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock) (Arachnida: Amblypygi), and its evolutionary significance. Zoological Journal of the Linnean Society 126: 81–116.

Shultz, J.W. 2000. Skeletomuscular anatomy of the harvestman *Leiobunum aldrichi* (Weed 1893) (Arachnida: Opiliones) and its evolutionary significance. Zoological Journal of the Linnean Society 128:401–438.

Shultz, J.W. & J.C. Regier. 2000. Phylogenetic analysis of arthropods using two nuclear-protein encoding genes supports a crustacean + hexapod clade. Proceedings of the Royal Society of London B 267:1011–1019.

Snodgrass, R.E. 1952. A Textbook of Arthropod Anatomy. Comstock Publishing Co., Ithaca, New York.

Telford, M.J. & R.H. Thomas. 1998. Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. Proceedings of the National Academy of Sciences USA 95: 10671–10675.

Tiegs, O.W. 1947. The development and affinities of the Pauropoda, based on a study of *Pauropus sylvaticus*. Quarterly Journal of Microscopical Science, 3rd Series 88:165–336.

Vachon, M. 1945. Remarques sur les appendices du prosoma des Limules et leur arthrogenèse. Archives de Zoologie Expérimentale et Générale 84:271–300.

Verhoeff, K.W. 1934. Symphyla und Pauropoda. Pp. 1–200, *In* Bronns Klassen und Ordnugen des Tierreichs, Vol. 5. Arthropoda, Part 2. Myriapoda, Book 3. (H.G. Bronn, ed.). Akadmische Verlagsgesellschaft m.b.H., Leipzig.

Versluys, J. & R. Demoll. 1922. Das *Limulus*-Problem. Die Verwandtschaftsbezeihungen der Merostomen und Arachnoiden unter sich und mit anderen Arthropoden. Ergebnisse und Fortschritte der Zoologie 5:67–388.

Weygoldt, P. 1979. Significance of later embryonic stages and head development in arthropod phylogeny. Pp. 107–135, *In* Arthropod Phylogeny. (A.P. Gupta, ed.). Van Nostrand Reinhold, New York.

Weygoldt, P. 1998. Evolution and systematics of the Chelicerata. Experimental & Applied Acarology 22:63–79.

Weygoldt, P. & H.F. Paulus. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. Zeitschrift für Zoologicshe Systematik und Evolutionsforschung 17:85–116, 77–200.

Wheeler, W.C. & C.Y. Hayashi. 1998. The phylogeny of the extant chelicerate orders. Cladistics 14:173–192.

Whitehead, W.F. & J.G. Rempel. 1959. A study of the musculature of the black widow spider, *Latrodectus mactans* (Fabr.). Canadian Journal of Zoology 37:831–870.

Wyse, G.A . & N.K. Dwyer. 1973. The neuromuscular basis of coxal feeding and locomotory movements in *Limulus*. Biological Bulletin 144: 567–579.

Yamasaki, T., T. Makioka & J. Saito. 1988. Morphology. Pp. 69–132. *In* Biology of Horseshoe Crabs. (K. Sekiguchi, ed.). Science House, Tokyo.

A NEW SPECIES OF *DIPLOCENTRUS* (SCORPIONES, DIPLOCENTRIDAE) FROM TEXAS

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ABSTRACT. *Diplocentrus lindo* new species, from west Texas, USA, central Nuevo Léon and northern Coahuila, México is described. This description is based on the morphological examination of 199 specimens from nine Texas counties and the Mexican states of Coahuila and Nuevo Léon. This species represents the third *Diplocentrus* known from the state of Texas, has a wider distribution than *D. diablo* and *D. whitei*, and it exhibits a marked range in adult size.

Keywords: *Diplocentrus lindo*, new species, scorpion

The genus *Diplocentrus* Peters 1861 is a poorly understood assemblage of burrowing scorpions known primarily from meso-America reaching its northern range limit in Arizona, New Mexico, and Texas in the United States. Species of *Diplocentrus* reported from Texas include *D. whitei* Gervais 1844, *D. diablo* Stockwell & Nilsson 1987, and *D. keyserlingii* Karsch 1880. *Diplocentrus whitei* is common in the Big Bend region of Texas and adjacent Mexico (Stockwell & Nilsson 1987; Sissom & Fet 2000). *Diplocentrus diablo* is known from the lower Rio Grande Valley from Webb County to Starr County (Stockwell & Nilsson 1987). *Diplocentrus keyserlingii* is found only in Oaxaca, Mexico (Sissom 1994). Records of this species from Texas (Ewing 1928; Gertsch 1939; Rowland & Reddell 1976; Fet et al. 2000) are referable to the new species described below.

METHODS

The measurements and terminology follow those of Stahnke (1970), except for trichobothriotaxy, which follows that of Vachon (1974), metasomal and pedipalpal carination, which follows that of Francke (1978), and hemispermatophore structure, which is modified from Vachon (1952). The measurements reported herein differ from Stahnke (1970) as

follows: in measuring the pedipalp chela, the depth is the greatest measurement between the dorsomarginal carina and ventromedian carina, chela width is the narrowest measurement between the digital carina and the internomedian carina, and chela length is measured from the basal-most edge of the external face at the proximal end of the digital or external secondary carina to the distal tip of the fixed finger. All measurements were made to the nearest 0.05 mm using a dissecting microscope equipped with an ocular micrometer.

Paraxial organs were dissected from males using iris scissors and forceps as described by Lamoral (1979). The hemispermatophores were dissected from the surrounding tissues and observed in 70% ethanol.

Letter codes used in the text to indicate the collections from which specimens were obtained are given in the acknowledgments. Specimens from the author's (SAS) collection are listed SAS.

Diplocentrus lindo new species
Figs. 1–9

Diplocentrus whitei Banks 1900: 424 (in part); Pocock 1902: 3, 4 (in part); Rowland & Reddell 1976: 5 (in part) (all misidentified).

Diplocentrus keyserlingi Ewing 1928: 5, 6; Gertsch 1939: 17; Rowland & Reddell 1976: 5 (all misidentified).

Diplocentrus linda Brown & Formanowicz 1996: 41, 42, 44, 45; Kovařík 1998: 130; Fet et al. 2000: 597 (NOMEN NUDUM).

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[1] *The views of the author do not represent the views of the Department of the Army or the Department of Defense.*

Figure 1.—*Diplocentrus lindo*, adult male paratype (left) from 5 mi. N of Sanderson, Terrell County, Texas, USA, and adult female paratype (right) from 0.5 mi. S of Langtry, Val Verde County, Texas, USA, dorsal aspect.
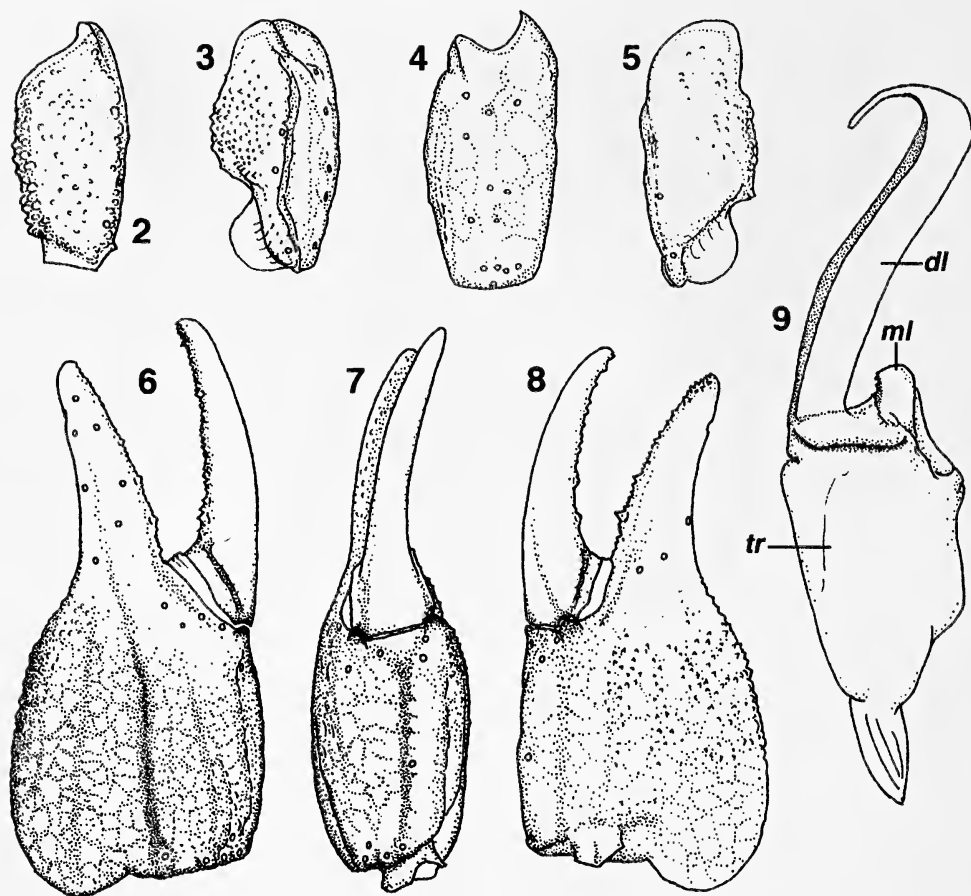
Type data.—Holotype male from 5 miles north of Sanderson, Terrell County, Texas, 15 June 1974 (Linda Draper, Mont A. Cazier, Oscar F. Francke), deposited in the American Museum of Natural History, New York. Paratypes are listed under specimens examined.

Etymology.—The specific epithet is Spanish for "pretty," and is used as a noun in apposition.

In their paper on reproductive investment in this species, Brown & Formanowicz (1996) used the manuscript name, "*Diplocentrus linda*," believing it to be an available name. Authorship was attributed to Stockwell with no date. The authors did not include a formal description of the species since it was not their intention to describe the species as new. The name thus fails to conform to the requirements of Article 13 of the International Code of Zoological Nomenclature, third edition (International Commission on Zoological Nomenclature 1985) and is therefore a nomen nudum by definition (Fet et al. 2000).

Diagnosis.—*Diplocentrus lindo* is distinguished from its most morphologically similar congener, *D. diablo* Stockwell & Nilsson 1987 from Texas, USA and Tamaulipas, Mexico, by

its slightly higher telotarsal spine formula (4/5:5/5-6:6/7:6/7 in *D. lindo*, 4/4:4/5:5/6:5/6 in *D. diablo*) and slightly longer fixed chela finger length (chela length/fixed finger length 2.29–2.50 in males and 2.33–2.59 in females in *D. lindo*, 2.31–2.37 in males and 2.21–2.33 in females in *D. diablo*). *Diplocentrus lindo* and *D. diablo* are also widely allopatric in Texas. It differs from *D. colwelli* Sissom 1986 from central Nuevo Léon, Mexico by its slightly longer pedipalp chelae (chela length/depth 1.92–2.16 in *D. lindo*, 1.78–1.88 in males and 1.86–1.96 in females in *D. colwelli*), weaker reticulations on the pedipalp chelae, slightly lower telotarsal spine formula (4/5:5/5–6:6/7:6/7 in *D. lindo*, 5/5–6:5/6:6/7:6/7 in *D. colwelli*), and moderately dentate lateral margin of median lobe of the hemispermatophore (vestigially dentate in *D. colwelli*). *Diplocentrus lindo* is distinguished from *D. ferrugineus* Fritts & Sissom 1996 (from southern Nuevo Léon) by having a lower telotarsal spine formula (4/5:5/5–6:6/7:6/7 in *D. lindo*, 5/5:6/6:7/7:7/7–8 in *D. ferrugineus*), a higher chela length/depth ratio in males (mean chela length/depth 2.00 in both sexes for *D. lindo*, 2.19–2.28 in *D. ferrugineus* males, 2.02 for

Figures 2–9.—*Diplocentrus lindo*, adult male holotype from 5 miles north of Sanderson, Terrell County, Texas, USA. 2–8. Right pedipalp; 2. Femur, dorsal aspect; 3. Patella, dorsal aspect; 4. Patella, external aspect; 5. Patella, ventral aspect; 6. Chela, external aspect; 7. Chela, ventral aspect; 8. Chela, internal aspect. 9. Right hemispermatophore, lateral aspect. *Abbreviations: dl* = distal lamella, *ml* = median lobe, *tr* = trunk. Not to scale.

females), and is much lighter in color than in *D. lindo*. *Diplocentrus lindo* is easily distinguished from *D. whitei* Gervais 1844 from Texas, USA and Coahuila, Mexico, by its lower telotarsal spine formula (4/5:5/5–6:6/7:6/7 in *D. lindo*, 5–6/7:6/7–8:7/8:7/8 in *D. whitei*), its lower pectinal tooth counts (males 11–15, females 9–13, for *D. lindo*; males 16–20, females 14–18, for *D. whitei*), and shorter, stouter pedipalps (mean chela length/depth 2.00 in both sexes for *D. lindo*, 2.60 in males and 2.17 in females for *D. whitei*). *Diplocentrus lindo* is generally darker in color than *D. spitzeri* Stahnke 1970 from Arizona, USA and Sonora, Mexico, and *D. peloncillensis* Francke 1975 from Arizona and New Mexico, USA. *Diplocentrus lindo* also has lower telo-

tarsal spine formulas, especially on telotarsi I and II (4/5:5/5–6:6/7:6/7 in *D. lindo*, 6/6:6/6–7:7/7:7/7 in *D. spitzeri*, 5/6:6/6–7:6/7:6/7 in *D. peloncillensis*).

Description.—*Male:* Color brown with variable dark brown marbling. Carapace smooth to minutely granular interspersed with a few larger granules anteriorly and laterally; prosomal venter lustrous, punctate; pectinal tooth count 11 to 15 (mode 14). Mesosomal tergites moderately granular; tergite VII acarinate, moderately bilobate, coarsely granular. Sternites lustrous; sternite VII with submedian and lateral carinae weak, smooth on posterior one-half to one-fourth.

Metasoma moderately hirsute; intercarinal spaces lustrous, finely punctate. Dorsolateral

carinae weak, vestigially granulose on segments I-IV. Lateral supramedian carinae moderate, granulose on segments I-IV. Lateral inframedian carinae moderate on segment I; weak on II and III; vestigial on IV; granulose on all segments. Ventrolateral carinae moderate, granulose on segments I-III; weak, granulose on IV. Ventral submedian carinae moderate, vestigially granulose on segments I-II; weak, vestigially granulose on III; obsolete on IV. Metasomal segment V dorsolateral carinae weak, smooth; lateromedian carinae weak, granular; ventrolateral, ventromedian and ventral transverse carinae moderate with a single row of large tubercles; anal subterminal carina moderate, tuberculate; anal terminal carina weak, crenulate. Telson smooth with a few tubercles on ventral anterior margin; moderately setose.

Pedipalps robust, orthobothriotaxic C (Vachon 1974, figs. 11–17). Femur with dorsal face sparsely granular; internal face with moderately dense tubercles; ventral and external faces weakly granular to smooth; dorsointernal carina moderate, granulose; dorsoexternal carina moderate with large granules proximally, obsolete distally; ventroexternal carina obsolete; ventrointernal carina weak, irregularly tuberculate. Patella with ventral and external faces weakly to vestigially reticulate; internal face moderately granular; basal tubercle moderately strong, rounded, moderately granular; dorsomedian carina moderate, smooth; ventroexternal carina moderate, smooth; ventrointernal carina weak to moderate, tuberculate; other carinae obsolete. Chela with dorsal and external faces moderately reticulate; internal and ventral faces weakly reticulate; dorsomarginal carina weak to moderate, granular; dorsal secondary carina vestigial; digital carina strong; external secondary carinae weak; ventroexternal carina obsolete; ventromedian carina strong; ventrointernal carina moderate; three internal carinae weak to vestigial, granular. Legs typical for genus. External faces with weak to moderately dense granulation. Modal telotarsal spine formula 4/5:5/5–6:6/7:6/7. Distal lamella of hemispermatophore not noticeably elongate. Lateral external margin of median lobe moderately dentate (fig. 18). Measurements of holotype male (L = length, W = width, D = depth). Total L, 43.30. Carapace L, 5.65. Mesosoma L, 14.00. Metasoma L, 23.65. Metasomal segments L/W/D: I, 2.90/3.10/2.30; II, 3.20/2.70/2.20; III, 3.50/2.60/2.15; IV, 4.10/2.55/2.10; V, 5.30/2.05/1.90. Telson: L, 4.65; vesicle L/W/D, 3.65/2.10/1.75; aculeus L, 1.00. Chelicera: chela L/W, 2.85/1.20; fixed finger L, 1.05; movable finger L, 1.70. Pedipalp: femur L/W/D, 4.50/2.05/1.70; patella L/W/D, 4.65/2.25/2.50; chela L/W/D, 9.90/2.80/4.80; fixed finger L, 4.30; movable finger L, 6.10.

Female: Similar to male except as follows. Tergites sparsely granular to smooth; pedipalpal and metasomal carinae weaker, reticulate pattern vestigial to obsolete; pectinal tooth counts 9 to 13 (mode 10). Sexes are morphometrically similar; carapace wider than long; pedipalp chela length/depth ratio 1.9–2.2; metasomal segment I wider than long; remaining segments longer than wide.

Measurements of a paratype female from 19 mi. S of Sheffield, Terrell County, Texas: Total L, 38.55. Carapace L, 5.20. Mesosoma L, 13.95. Metasoma L, 19.40. Metasomal segments L/W/D: I, 2.35/2.90/2.05; II, 2.60/2.50/2.10; III, 2.85/2.40/2.05; IV, 3.25/2.25/1.90; V, 4.25/1.95/1.85. Telson: L, 4.10; vesicle L/W/D, 3.20/2.15/1.70; aculeus L, 0.90. Chelicera: chela L/W, 2.65/1.30; fixed finger L, 1.00; movable finger L, 1.60. Pedipalp: femur L/W/D, 3.75/1.80/1.55; patella L/W/D, 4.15/1.90/2.05; chela L/W/D, 8.55/2.60/4.25; fixed finger L, 3.45; movable finger L, 5.05.

Variation.—*Diplocentrus lindo* displays a marked difference in overall size across its geographic range. In higher, cooler areas, such as the Davis Mountains of Texas, adults may be nearly half the size of individuals from lower, warmer localities. It was initially suspected that the two size classes represented different species. However, except for the difference in size, we have found no discernible variation between the groups. We compared the ranges, means, and standard deviations of six taxonomically important morphometric ratios from 20 small adult males and 20 large adult males and found no significant differences between the two groups, despite the difference in overall size. We subsequently pooled the data for all males. The ranges, means, and standard deviations of these six taxonomically important morphometric ratios from 40 adult males and 20 adult females are as follows: pedipalp chela length/depth: males 1.92–2.16, 2.00, 0.05; females 1.92–2.13, 2.00, 0.06. Pedipalp chela length/carapace

length: males 1.63–1.80, 1.70, 0.04; females 1.53–1.68, 1.62, 0.04. Pedipalp chela length/ pedipalp fixed finger length: males 2.29–2.50, 2.40, 0.06; females 2.33–2.59, 2.41, 0.07. Carapace length/pedipalp fixed finger length: males 1.33–1.53, 1.41, 0.06; females 1.39–1.69, 1.48, 0.08. Pedipalp fixed finger length/ pedipalp femur length: males 0.85–0.98, 0.90, 0.03; females 0.84–1.00, 0.94, 0.04. Pedipalp fixed finger length/metasomal segment V length: males 0.68–0.81, 0.76, 0.04; females 0.74–0.92, 0.85, 0.04.

Specimens ($n = 199$) varied in pectinal tooth counts as follows: in males, one comb had 11 teeth, 11 combs had 12 teeth, 78 combs had 13 teeth, 153 combs had 14 teeth, 27 combs had 15 teeth, and three combs were damaged or missing; in females, one comb had nine teeth, 70 combs had ten teeth, 37 combs had 11 teeth, 13 combs had 12 teeth, one comb had 13 teeth, and three combs were damaged or missing.

As in all *Diplocentrus* species, there is variation in telotarsal spine counts of *D. lindo*. We report the telotarsal spine counts from 183 specimens. Spine counts from both the right and left legs are reported for each specimen. For each leg, we report the number of spines in the row followed by the number of legs exhibiting that count (in parentheses). Missing or damaged telotarsal rows are indicated by X. Leg I: prolateral row - 2 (2), 3 (7), 4 (327), 5 (25), X (5); retrolateral row - 3 (4), 4 (42), 5 (312), 6 (2), 7 (1), X (5). Leg II: prolateral row - 3 (1), 4 (10), 5 (344), 6 (4), 7 (1), X (6); retrolateral row - 2 (1), 3 (1), 4 (10), 5 (121), 6 (226), X (7). Leg III: prolateral row - 4 (2), 5 (48), 6 (303), 7 (10), 10 (1), X (2); retrolateral row - 5 (1), 6 (53), 7 (303), 8 (6), 11 (1), X (2). Leg IV: prolateral row - 4 (1), 5 (29), 6 (308), 7 (28), X (3); retrolateral row - 4 (1), 5 (1), 6 (53), 7 (290), 8 (18), X (3).

Distribution.—This species is widely distributed throughout west Texas and is recorded from Culberson, Reeves, Jeff Davis, Pecos, Upton, Crockett, Brewster, Terrell, and Val Verde counties. This species is also known from the states of Coahuila and Nuevo Léon in Mexico. *Diplocentrus lindo* is usually found on rocky slopes. Individuals may be found in burrows beneath large stones and other surface objects.

Specimens examined.—USA: *TEXAS: Brewster*

County, Alpine, 5 June 1942 (E.S. Ross), 3 males 1 female (CAS); Alpine, 16 July 1949 (B.H. Warnock), 1 male (CAS); Alpine, 23 April 1964 (J. Scudday), 1 male (CAS); Alpine, 27 April 1964 (C. Babcock), 1 female (CAS); Alpine, 26 November 1964 (J. Scudday), 1 female (CAS); Alpine, 14 June 1965 (J. Scudday), 1 female (CAS); 5 mi. S Alpine, 12 July 1955 (S.A. Minton), 1 male (CAS); 5.5 mi. S Alpine, 19 August 1968 (S.C. Williams, M.M. Bentzien, J. Bigelow), 2 females (CAS); 6 mi. S of Alpine, 30 June 1965 (M.H. Muma), 1 female (CAS); 6 mi. S of Alpine, 27 July 1978 (O.F. Francke, J.V. Moody), 4 females (AMNH); 8 mi. S Alpine, Hwy. 118, 25 September 1964 (J. Scudday), 2 females (CAS); 8 mi. S Alpine, 26 November 1964 (J. Scudday), 7 females (CAS); 10–12 mi. S Alpine, 4/11 October 1964 (J. Scudday), 5 males 2 females 2 immatures (CAS); 10 mi. SW of Alpine, 11 August 1966 (A. Jung, K. Hom), 1 male (AMNH); 10 mi. SW of Alpine, 11 August 1966 (T. Briggs, A. Jung, K. Hom), 6 females (CAS); 12 mi. S Alpine, Hwy. 118, 5/10 October 1965 (Rogers, Freels), 2 females (CAS); 22 mi. S Alpine, Babcock Ranch, 25/26 April 1964 (S. Sikes), 2 females (CAS); 22 mi. S Alpine, Babcock Ranch, 27 April 1964 (C.E. Babcock), 1 male 2 females (CAS); 23 mi. S Alpine, Babcock Ranch, 15 March 1964 (C.E. Babcock), 1 male 2 females (CAS); 25 mi. S Alpine nr. Calamity Cr., 15 April 1964 (T. Watson), 1 female (CAS); 5 mi. E Lajitas, 1 August 1986 (R.W. Manning, R. Hollander), 1 male (WDS); Paisano (Biological Expeditions, U. S. Dept. of Agriculture), 7 July 1890 (W. Lloyd), 1 female (USNM); Black Gap Wildlife Area, 30 July 1955 (W.G. Degenhardt), 1 male (AMNH); Black Gap Refuge, Norton Tank, 30 August 1960 (W.G. Degenhardt), 1 female (CAS); 41 mi. N Panther Jct., Hwy. 385, 17 August 1968 (S.C. Williams, M.M. Bentzien, J. Bigelow), 3 males 4 females (CAS); Big Bend N.P., 1959 (H.L. Stahnke), 1 male (CAS); Big Bend N.P., Grapevine Hills, 17 August 1968 (M.A. Cazier, J. Bigelow), 1 male (AMNH); Big Bend N.P., 13. 2 mi. SE Panther Jct., 17 August 1968 (S.C. Williams, M.M. Bentzien), 2 males (CAS); Big Bend N.P., Kibbe Spr., 24 July 1956 (H.L. Stahnke), 2 females (CAS); Big Bend N.P., Oak Spr., 30 July 1956 (H.L. Stahnke), 1 female (CAS); Big Bend N.P., Window Trail, 19 July 1956 (R. Curbow), 1 female (CAS); Big Bend N.P., Chisos Mts., no date (no collector), 2 females (AMNH); Big Bend N.P., Chisos Basin, CCC Camp, 25–30 July 1937 (Necker), 1 female (AMNH); Big Bend N.P., Laguna, Mt. Emory, 12 April 1937 (no collector), 1 female (AMNH); Big Bend N.P., Chisos Mts., foot of Emery Mts., 6 July 1938 (E. Shaw, J. & R. Schmidt), 1 female (CAS); Big Bend N.P., Chisos Mts., foot of Mt. Emory, 6 July 1938 (B.H. & E. Shaw), 1 male 1 female (CAS); Big Bend N.P., Chisos Mts., 28 May 1952

(M.A. Cazier, W. J. Gertsch, R. Schrammel), 2 females (AMNH); Big Bend N.P., Chisos Mts., Green Gulch, 5 April 1955 (S.A. Minton), Big Bend N.P., Chisos Mts. Basin, 1 July 1956 (E. Steele), 1 male (CAS); Big Bend N.P., Chisos Mts. Upper Basin, 30 July 1955 (H.L. Stahnke), 1 male (CAS); Big Bend N.P., Upper Basin, 21/25 July 1956 (H.L. Stahnke), 1 male 1 female (CAS); Big Bend N.P., Chisos Basin, 5 August 1962 (C.A. Triplehorn), 1 male (CAS); Big Bend N.P., Chisos Basin, 26 May 1965 (K.W. Haller), 2 males (AMNH); Big Bend N.P., Chisos Basin, 27 August 1965 (C. Parrish), 1 male 2 females (CAS); Big Bend N.P., Chisos Basin Pass, 28 July 1978 (O.F. Francke, J.V. Moody), 1 female (AMNH); Big Bend N.P., Chisos Basin, 29 July 1978 (O.F. Francke, J.V. Moody), 1 female (AMNH); Big Bend N.P., Chisos Basin, 9 August 1979 (O.F. Francke), 1 female (AMNH); Big Bend N.P., Juniper Canyon, July 1921 (no collector), 1 male 5 females (AMNH); Big Bend N.P., Pine Canyon, 10 August 1979 (Francke, Moody, Merickel), 1 male 1 female (AMNH); Big Bend N.P., Pine Canyon, 10 August 1979 (Francke, Moody, Merickle), 1 female with young (AMNH); Big Bend N.P., Boquillas Canyon, 27 January 1973 (C. McConnell), 1 female (AMNH). *Crockett County:* 11 mi. N of Iraan, 29 September 1985 (S.A. Stockwell), 1 male 1 female (SAS); 10 mi. N of Iraan, 15 September 1985 (S.A. Stockwell), 6 females (SAS); 5 mi. N, 4 mi. W Iraan, 30 June 1986 (Manning, Hollander), 2 males (WDS); 15 mi. E of Iraan, 14 September 1985 (S.A. Stockwell), 1 male (SAS); 45 mi. NW of Ozona, 21 March 1978 (O.F. Francke, T.B. Hall, J.V. Moody), 2 females (AMNH). *Culberson County:* 8 January 1981 (G. Zolnerowich), 2 females (MWSU); 4 mi. NNE of Kent, 14 March 1981 (N.V. Horner), 2 males 1 female (MWSU); 6 mi. N of Kent, 20 March 1985 (no collector), 1 female (MWSU); 9 mi. N of Kent, 19 April 1980 (W.W. Dalquest), 1 female (MWSU); 31.8 mi. NE of Van Horn, 2 July 1978 (Francke, Hall, Moody), 1 male (AMNH). *Jeff Davis County:* 15 April 1968 (F. Horne), 2 males 6 females (CAS); Davis Mts., Fort Davis Quad., Cottonwood Springs, 27 May 1916 (F.M. Gaige), 1 female (UMMZ); Davis Mts., Fort Davis Quad., Cottonwood Springs, 5 June 1916 (F.M. Gaige), 1 female (UMMZ); Davis Mts., Fort Davis Quad., Cottonwood Springs, 7 June 1916 (F.M. Gaige), 1 male 4 females (UMMZ); Davis Mts., Fort Davis Quad., 12 June 1916 (F.M Gaige), 1 female (UMMZ); Davis Mts., Fort Davis Quad., Two Spring Canyon, 28 June 1916 (F.M. Gaige), 1 male 1 female (UMMZ); Davis Mts., Fort Davis Quad., 6 July 1916 (F.M. Gaige), 1 male (UMMZ); Davis Mts., Fort Davis Quad., Maple Canyon, 8 July 1916 (F.M. Gaige), 5 females 2 immatures (UMMZ); Davis Mts., Fort Davis Quad., Cherry Canyon, 9 July 1916 (F.M. Gaige), 1 female (UMMZ); Davis Mts., Fort Davis

Quad., 14 July 1916 (F.M. Gaige), 1 female (UMMZ); Davis Mts., 9 May 1951 (O. Bryant), 1 male (CAS); Davis Mts. State Park, no date (O.F. Francke, J.V. Moody), 1 male (AMNH); Davis Mts. State Park, 5 mi. N Ft. Davis, 26 April 1964 (C. Babcock), 1 male (CAS); Davis Mts. State Park, 20 June 1970 (M.A. Cazier, L. Draper, O.F. Francke), 46 males 7 females (AMNH); Davis Mts. State Park, Limpia Canyon Campground, 5 June 1974 (L. Draper, M.A. Cazier, O.F. Francke), 37 males 10 females (AMNH); Davis Mts. State Park, 9 June 1978 (O.F. Francke), 3 males (WDS); Davis Mts. State Park, 1 March 1985 (S.A. Stockwell, J.M. Steele), 1 male 1 females (SAS); 2 mi. W of Fort Davis, 22 April 1970 (A. Schoenhor, W.L. Minckley), 1 male 2 females (AMNH); 4 mi. W of Fort Davis, 6 June 1978 (O.F. Francke) (WDS); 9 mi. N of Fort Davis, 22 June 1970 (W. Seifert), 1 male (MWSU); 8 mi. E of McDonald Observatory, no date (N.V. Horner), 1 male (MWSU); 20 km S of Toyahvale, 13 March 1977 (D. Holub, K. Douglas), 1 male, 1 female (MWSU). *Pecos County:* 10 mi. N of Ft. Stockton on Will Banks Ranch, 27 December 1966 (B. Winokur), 4 females (CAS); 30 mi. S of Ft. Stockton, Glass Mts., 7 June 1974 (L. Draper, M.A. Cazier, O.F. Francke), 2 males (AMNH); Sheffield, Pecos River Bluff, 7 July 1968 (M.H. and E.U. Muma), 1 female with three first instar young (CAS); 4 mi. E of Sheffield, Pecos River, 7 June 1974 (M.A. Cazier, L. Draper, O.F. Francke), 8 males 7 females (AMNH); 15 mi. N of Sanderson, 3 June 1970 (W. Seifert), 1 female (MWSU); 20 mi. W of Sanderson, 2 September 1983 (W.D. & J.C. Sissom), 1 female (WDS). *Reeves County:* 22 mi. SW of Toyah, 3 October 1983 (D. Foster), 1 male (WDS); Balmorhea State Park, 26 August 1971 (K., M., and M.A. Cazier), 2 males 1 female (AMNH); Balmorhea State Park, June 1979 (Moody, Merickel), 2 females (AMNH). *Terrell County:* Sheffield, Pecos R. Bluff, 7 July 1968 (M.H. and E.U. Muma), 1 female (CAS); 19 mi. S of Sheffield, Blackstone Ranch, 16 May 1958 (W.H. McAlister), 1 female (TMM), 19 mi. S of Sheffield, 8 June 1974 (O.F. Francke), 6 immatures (AMNH); 19 mi. S of Sheffield, 15 June 1974 (L. Draper, M.A. Cazier, O.F. Francke), 2 males 2 females (AMNH); Pecos River and Independence Creek, Chandler Ranch, 27–28 June 1968 (W.L. Minckley), 2 males (AMNH); 1 mi. S Pecos County line, 4 June 1986 (Manning, Hollander), 1 male 1 juvenile (WDS); 6.3 mi. NW Sanderson, 20 November 1960 (D. Campbell, H. Harris), 1 female (AMNH); 5 mi. N of Sanderson, 8 June 1974 (L. Draper, M.A. Cazier, O.F. Francke), 3 males (AMNH); 5 mi N of Sanderson, 15 June 1974 (L. Draper, M.A. Cazier, O.F. Francke), 10 males (AMNH); 4 mi. E of Dryden, 4 September 1939 (D. and S. Mulaik), 3 females (AMNH); 21 mi. N of Dryden, 2 July 1970 (W. Seifert), 1 male (MWSU); *Upton County*, 3 mi.

S, 5 mi. E McCamey, 7 June 1986 (Manning, Hollander), 2 males 1 juvenile (WDS). *Val Verde County:* 20 mi S of Juno, 2 May 1970 (W. Seifert), 2 females (MWSU); 21 mi. N of Comstock, 14 September 1985 (S.A. Stockwell), 2 males 1 female (SAS); 19 mi. N of Comstock, 14 April 1973 (J. Cooke), 1 male 2 females (AMNH); 15 mi. N Comstock, 22 June 1971 (no collector), 1 male 2 females (CAS); 10 mi. N Comstock, 22 June 1971 (no collector), 1 male 2 females (CAS); 7 mi. N Comstock, 12 July 1986 (Manning, Hollander), 1 female (WDS); 0.5 mi. NW of Comstock, 8 May 1968 (T. Walker), 1 female (AMNH); 10 mi. W of Comstock, Pecos River, 2 September 1983 (W.D. & J.C. Sissom), 1 male (WDS); 11 mi. W of Comstock, 28 August 1970 (F. & J.M. Davidson), 2 males (CAS); 21 mi. N of Langtry, 14 April 1973 (T.R. Mollhagen), 1 female (AMNH); 5 mi. N of Langtry, 15 April 1973 (J. Cooke), 1 male 1 female (AMNH); 3 mi. N of Langtry, 3 November 1984 (J. Reddell, M. Reyes), 1 female (TMM), Langtry, 26 June 1971 (E. Tombellin), 1 female (AMNH); 0.5 mi. S of Langtry, 14 June 1974 (L. Draper, M.A. Cazier, O.F. Francke), 5 males 7 females (AMNH); 2 mi. SSE Langtry, 7 June 1974 (L. Draper, M.A. Cazier, O.F. Francke), 1 female (AMNH); 3 mi. W of Langtry, Rattlesnake Canyon, 30 April 1983 (F.L. Rose), 1 female with young (AMNH). **MEXICO:** *COAHUILA:* 10 km SE Musquiz, 24 June 65 (J. Reddell), 1 female (TMM). *NUEVO LÉON:* 4 mi. S of Bustamante, 26 March 1964 (B. Russell), 1 male (AMNH); 9 mi. E of Mex. 57 on Galeana Road, March 1968 (T. Walker), 1 male (AMNH); 2 mi. NE of Villa de Garcia, 19 August 1984 (Sissom, Myers, Born), 1 male (WDS).

ACKNOWLEDGMENTS

LITERATURE CITED

Banks, N. 1900. Synopses of the North American invertebrates. IX. The scorpions, solpugids and pedipalpi. American Naturalist 34:421–427.

Brown, C.A. & D.R. Formanowicz, Jr. 1996. Reproductive investment in two species of scorpion, *Vaejovis waueri* (Vaejovidae) and *Diplocentrus linda* (Diplocentridae), from west Texas. Annals of the Entomological Society of America 89:41–46.

Ewing, H.E. 1928. The scorpions of the western part of the United States, with notes on those occurring in northern Mexico. Proceedings of the United States National Museum 73:1–24.

Fet, V., W.D. Sissom, G. Lowe & M.E. Braunwalder. 2000. Catalog of the Scorpions of the World (1758–1998). The New York Entomological Society, New York, 690 pp.

Francke, O.F. 1978. Systematic Revision of Diplocentrid Scorpions (Diplocentridae) from Circum-Caribbean Lands. Special Publications of the Museum, Texas Tech University, No. 14, 92 pp.

Gertsch, W.J. 1939. Report on a collection of Arachnida from the Chisos Mountains. Contributions to the Baylor University Museum, Waco, Texas 24:17–26.

Kovařík, F. 1998. [Stiri (Scorpions). Madagascar.] Jihlava. 175 pp. (in Czech).

Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). Annals of the Natal Museum 23:497–784.

Pocock, R.I. 1902. Arachnida: Scorpiones, Pedipalpi, et Solfugae. *In:* Biologia Centrali-Americana (Zoologia). London, Taylor & Francis. 71 pp.

Rowland, J.M. & J.R. Reddell. 1976. Annotated checklist of the arachnid fauna of Texas (excluding Acarida and Araneida). Occasional Papers of the Museum, Texas Tech University 38:1–25.

Sissom, W.D. 1994. Systematic studies on *Diplocentrus keyserlingii* and related species from central Oaxaca, Mexico (Scorpiones, Diplocentridae). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut Berlin 70:257–266.

Sissom, W.D. & V. Fet. 2000. Family Diplocentridae Karsch, 1880. Pp. 329–354. *In:* Catalog of the Scorpions of the World (1758–1998) (Fet, V., W.D. Sissom, G. Lowe, & M.E. Braunwalder, eds.). The New York Entomological Society, New York.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. Entomological News 81:297–316.

Stockwell, S.A. & J.A. Nilsson. 1987. A new species of *Diplocentrus* Peters from Texas (Scorpiones, Diplocentridae). Journal of Arachnology 15:151–156.

Vachon, M. 1952. Ètudes Sur Les Scorpions. Publications de l'Institut Pasteur d'Algérie, Algiers. 462 pp.

Vachon, M. 1973 (1974). Ètude des caractéres utilisés pour classer les familles et les genres de scorpions. 1. La trichobothriotaxie en Arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez lez Scorpions. Bulletin du museum national d'histoire naturelle (Paris), sér. 3, 104: 857–958.

NOTES ON THE GENUS *SCYTODES*
(ARANEAE, SCYTODIDAE)
IN CENTRAL AND SOUTH AMERICA

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ABSTRACT. In this study we present a redescription of *Scytodes championi*, *S. romitii* and *S. guttipes*. Seven species are newly described: *S. panamensis* from Panama; *S. vaurieorum* and *S. chiquimula* from Guatemala; *S. cogu* and *S. armata* from Costa Rica; *S. tegucigalpa* and *S. zamorano* from Honduras. Four of these were described as variations of *S. championi* in a recent revision of the species of Central America. New records are presented for *S. championi*, *S. romitii*, *S. guttipes*, *S. gertschi* and *S. cubensis*.

The genus *Scytodes* Latreille 1804 has been intensively studied in the Neotropical region during the last two decades (Brignoli 1976; Alayón 1977, 1985, 1992; Valerio 1981; Brescovit & Höfer 1999; Brescovit & Rheims 2000; Rheims & Brescovit 2000). The genus has a worldwide distribution with several synanthropic species (Brescovit & Rheims 2000). To date, at least 42 species in the Neotropical region are considered valid.

During a preliminary study of the Brazilian *Scytodes*, we observed that *Scytodes romitii*, described by Caporiacco (1947) from Guyana, was very common in the north and northeast of the country. This species, herein redescribed, is very similar to *S. championi* F.O.P.-Cambridge 1899, previously known from Central America, differing only slightly in the morphology of the male and female genitalia. The similarity between these species was so accentuated that it became necessary to reconsider earlier records, for the State of Amazonas, of *S.* cf. *championi* (see Höfer 1990) and *S. championi* (see Brescovit & Höfer 1999).

Scytodes championi was originally described by F.O.P.-Cambridge (1899) for Chiriqui, Panama, and more recently redescribed by Valerio (1981). Valerio presented a series of variations for *S. championi* together with a revision of the Central American scytodid species. He also examined specimens identified as *S. guttipes* Simon 1893, by Banks

(1929) and considered them identical to *S. championi*. Nevertheless, he kept the name *championi* for the Central American forms due to the lack of type examination and general revisions. Nentwig (1993) followed Valerio's identifications and considered Banks's specimens as misidentifications.

Based on Valerio's paper and on the study of material from Central and north of South America we concluded that the *S. championi* sensu Valerio is, in fact, a group of four different species, based on morphological differences of male and female genitalia as well as carapace basic coloration pattern. Although Brignoli (1976, figs. 20–25) argues that *S. thoracica* (Latreille 1802) and *S. strandi* Spassky 1941 present a high degree of genitalic variation we do not consider this applicable to *S. championi* sensu Valerio (1981, figs. 16–18) since we observed a very constant pattern of genitalic morphology in all Central American species of what we could call the *"championi"* group.

In addition, we found that *S. championi* occurs in the Brazilian states of Amazonas, Roraima and Pará and is sympatric with *S. romitii* at least in the state of Amazonas. A redescription of *S. guttipes* is presented, confirming it as a valid species. Seven new *Scytodes* species are described for Central America and new records and illustrations are presented for *Scytodes gertschi* Valerio 1981 and for the male of *S. cubensis* Alayón 1977.

The material examined belongs to the following institutions: AMNH, American Museum of Natural History, New York (N.I. Platnick); BMNH, The Natural History Museum, London (J. Beccaloni); CEPLAC, Centro de Pesquisas do Cacau, Itabuna, Bahia (P.S. Terra); IBSP, Instituto Butantan, São Paulo (A.D. Brescovit); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus (C. Magalhães); MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (E.H. Buckup); MZS, Museo Zoologico de La Specola, Firenze (S. Whitman); MCTP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (A.A. Lise); MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, (L. Leibensperger); MNHN, Muséum National de Histoire Naturelle, Paris (C. Rollard); MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro (A.B. Kury); MZSP, Museu de Zoologia da USP, São Paulo (E. Cancello); SMNK, Staatliches Museum für Naturkunde Karlsruhe (H. Höfer). Despite our efforts, it was not possible to obtain Valerio's scytodid material, deposited in the Museo de Zoologia, Universidade de Costa Rica (MZUCR).

Descriptions and terminology follow Brescovit & Rheims (2000). All measurements are in mm. The female genitalia were submerged in lactic acid to study internal structures. Micrographs were obtained with a JEOL (JSM 840A) scanning electron microscope from the "Laboratório de Microscopia Eletrônica do Departamento de Física Geral do Instituto de Física da Universidade de São Paulo (USP)."

Scytodes championi F.O.P.-Cambridge
(Figs. 1, 2, 13–17)

Scytodes championi F.O.P.-Cambridge 1899: 51 (male lectotype and female paralectotype, here designated, from Chiriqui, Panama deposited in BMNH, examined); Roewer 1942: 329; Valerio 1981: 87, only figs. 7–9.

Diagnosis.—The males of *S. championi* resemble those of *S. romitii* and *S. panamensis* by the dorsal groove on the distal area of the palpal bulb, but differ by the strong median narrowing of the bulb and greater depth of the dorsal groove (Figs. 1, 2, 14). The female differs from females of the other species by the widely separated and almost transversally oriented positioning ridges (Fig. 16) and anterior pair of subtriangular seminal receptacles separated from the smaller posterior pair (Fig. 17).

Male. (MCTP 1828).—Carapace yellow with double U-shaped dark brown pattern and a pair of internal parallel light brown stripes (Fig. 13). Pedipalps yellow with longitudinal dorsal brown stripe. Labium and endites yellow with brownish margins. Sternum yellow with brown margins at base of legs and extending towards center along slight grooves. Legs yellow with three longitudinal brown stripes along ventral face of femora and longitudinal stains along tibiae and metatarsi. Abdomen cream colored with dorsal scattered black spots and pair of transversal posterior black bands (Fig. 13). Total length 3.50. Carapace, 1.75 long, 1.50 wide. Eye diameters: PME 0.12, ALE 0.12, PLE 0.14. Lateral eyes on tubercle. Chelicerae with subapical hyaline keel. Labium 0.20 long, 0.22 wide. Sternum 0.96 long, 0.80 wide. Leg measurements: I - femur 2.63/ patella 0.50/ tibia 3.00/ metatarsus 3.50/ tarsus 0.63/ total 10.26/ II - 2.13/ 0.50/ 2.25/ 2.50/ 0.38/ 7.76/ III - 1.50/ 0.38/ 1.25/ 1.50/ 0.50/ 5.13/ IV - 2.00/ 0.50/ 2.25/ 2.25/ 0.50/ 7.50. Palpal femur presenting stridulatory pick long and slender with rounded and projected socket. Cymbium with single apical slender spine (Fig. 14). Bulb 0.38 long. Distal area ventrally with anterior slightly sclerotized membrane (SM) followed by subtriangular pocket. (P; Figs. 2, 14). Abdomen 1.75 long, 1.50 wide, rounded, covered with slender hairs.

Female. (MCTP 1827).—Coloration with same basic pattern as male. Total length 3.38. Carapace, 2.00 long, 1.75 wide. Eye diameters: PME 0.12, ALE 0.14, PLE 0.12. Lateral eyes and chelicerae as in male. Labium 0.16 long, 0.22 wide. Sternum 1.12 long, 0.82 wide. Leg measurements: I - femur 2.00/ patella 0.50/ tibia 2.13/ metatarsus 2.50/ tarsus 0.50/ total 7.63/ II - 1.63/ 0.50/ 1.50/ 2.00/ 0.50/ 6.13/ III - 1.13/ 0.38/ 1.13/ 1.25/ 0.38/ 4.14/ IV - 1.75/ 0.50/ 1.75/ 1.75/ 0.50/ 6.25. Epigynal fovea very narrow. Positioning ridge semicircular (Fig. 16). Internal genitalia with two pairs of seminal receptacles, the smaller ones globose (Fig. 17). Abdomen 1.38 long, 1.25 wide, as in male.

Variation.—*Males:* Total length 3.00–4.63; carapace 1.63–3.25; femur I 2.38–6.25;
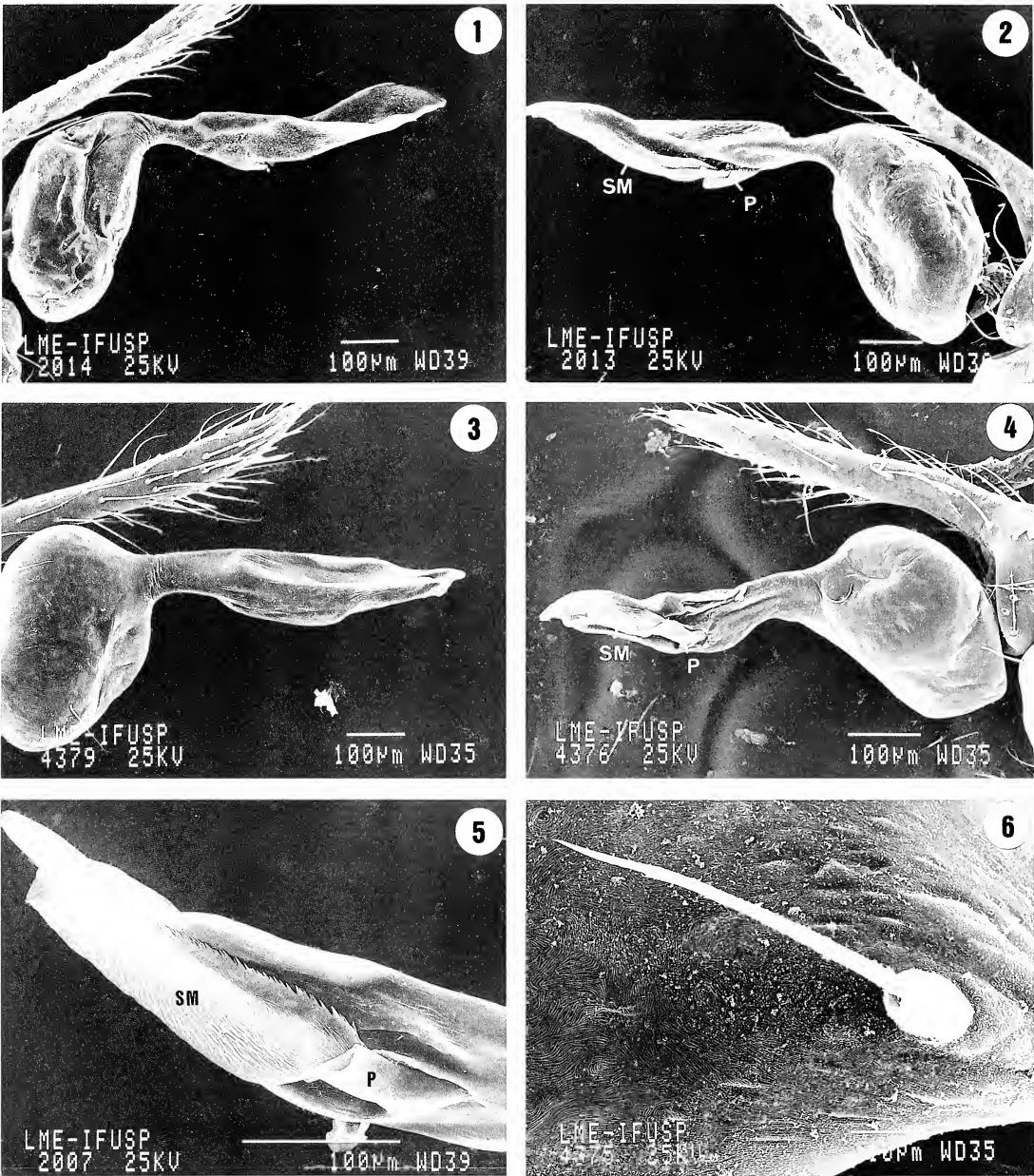
Figures 1–6.—1–2. *Scytodes championi* F.O.P.-Cambridge, male palp, prolateral view; 2. Retrolateral view. 3–6. *Scytodes romitii* Caporiacco. 3. Male palp, prolateral view; 4. Retrolateral view; 5. Distal area, retrolateral view; 6. Stridulatory pick (P = pocket, SM = sclerotized membrane).

bulb 0.32–0.50 (*n* = 15). *Females:* Total length 3.63–5.75; carapace 1.88–2.63; femur I 2.00–5.25 (*n* = 20). Coloration pattern and genitalic morphology constant.

Distribution.—Central America and northern South America.

Material examined.—NICARAGUA: *Jinotega:* Masawas (Waspuc River), 1♀, 17–30 Septem-

ber 1955, B. Malkin (AMNH); **GUATEMALA:** *Petén:* Tucuru, 2♂2♀, 12–13 July 1947, C. & P. Vaurie (AMNH); *Panzos:* 14–17 July 1947, C. Vaurie & P. Vaurie (AMNH); **EL SALVADOR:** *La Libertad:* La Libertad, 1♀, October 1959, N.L.H. Krauss (AMNH); **BELIZE:** *Toledo District:* 1♂, 7 April 1974, Goodnight (AMNH); **PANAMA:** *Canal Zone:* Barro Colorado Island, 1♂, 1 juv., 3 December 1965, R.X. Schick (AMNH); 1♀, 2 juvs.,
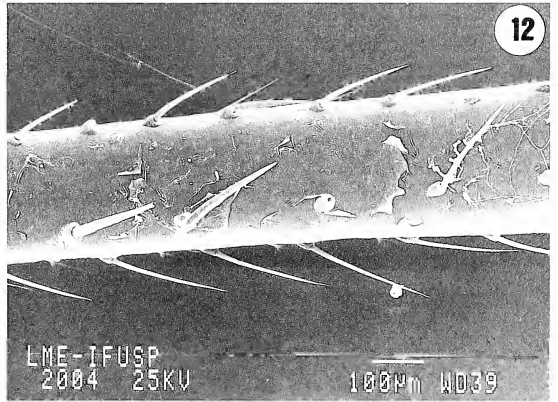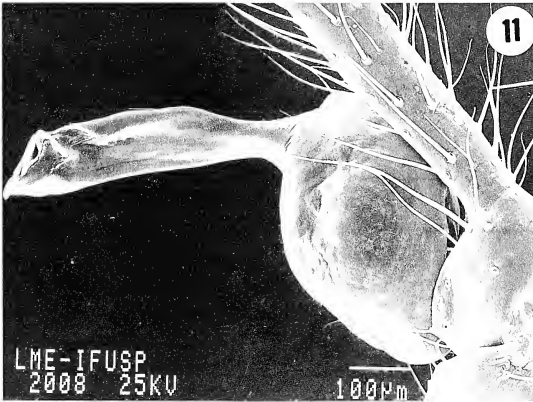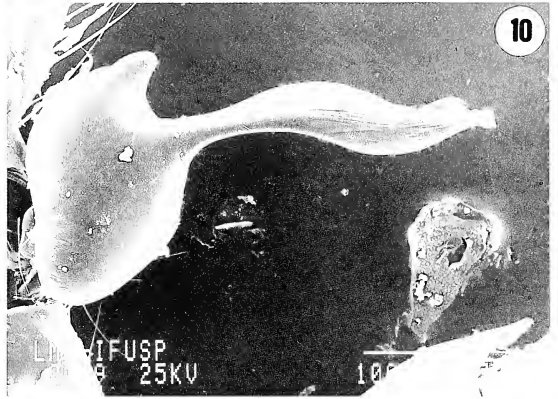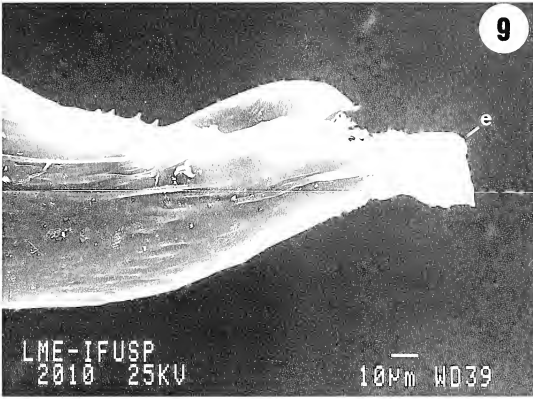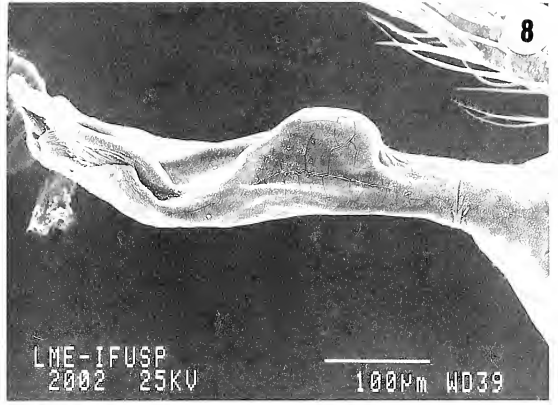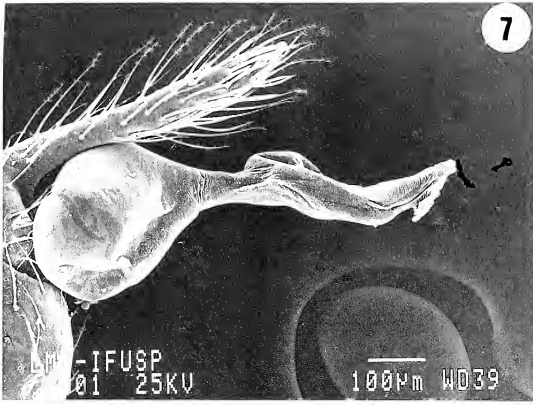
Figures 7–12.—7–8. *Scytodes panamensis* new species. 7. Male palp, prolateral view; 8. Distal area, retrolateral view. 9–10. *Scytodes tegucigalpa* new species. 9. Male palp, distal area (e = embolus opening); 10. Prolateral view. 11–12. *Scytodes armatus* new species. 11. Male palp, retrolateral view; 12. Male femur I, ventral spines.

April 1953, A.M. Nadler (AMNH); 3♀, 2 juvs., 20 April 1953, A.M. Nadler (AMNH); 1♀, 23 May 1952, T.C. Schneirla (AMNH); 2♀, 1928 (AMNH); 1♂, 3–20 April 1953, A.M. Nadler (AMNH); Barbacoas Islands, 1♂, 14 December 1965, R.X. Schick & M. Moody (AMNH); **BRAZIL:** *Roraima:* Ilha de Maracá, 1♂, 17 July 1987, A.A. Lise (INPA); 1♂1♀, 18 July 1987, A.A. Lise (INPA);

1♀, 19 March 1987, A.A. Lise (INPA); 1♂, 29 March 1987, A.A. Lise (INPA); 4♀, 6 juvs., 31 January–14 February 1992, A.A. Lise (MCTP 1827); 1♂3♀, 2 juvs., 31 January–14 February 1992, A.A. Lise (MCTP 1828); 1♀, 1 juv., 31 January–14 February 1992, M. Nascimento (MCTP 1966); (Estação Ecológica de Maracá), 20 March 1987, A.A. Lise (MCTP 17623); 1♂, 17 March

1987, A.A. Lise (MCN 17621); 1♂, 25 July 1987, A.A. Lise (MCN 17622); *Amazonas:* Manaus (Fazenda Esteio), 1♂, 15 October 1985, B.C. Klein (MCN 19876); São Gabriel da Cachoeira, Maturacá, 1♀, 13 October 1990, A.A. Lise (MCTP 1261); *Pará:* Santarém, Fátima de Urucurituba, 1♀, 24 January 1994, A.D. Brescovit (MCN 25354); 1♂, 24 January 1987, A.D. Brescovit (MCN 25030).

Scytodes romitii Caporiacco
(Figs. 3–6, 18–25)

Scytodes romitii Caporiacco 1947: 22 (female holotype from Diamont Point, East Demerara District, Guyana, 10.V.1936, deposited in MZS 519, examined); 1948: 626, figs. 17, 18; Brignoli 1983: 150.
Scytodes cf. *championi:* Höfer 1990: 175.
Scytodes championi: Brescovit & Höfer 1999: 105 (misidentification).

Diagnosis.—The males of *S. romitii* differ from the other species, here included, by the retrolateral medially-positioned ventral serrated sclerotized membrane (Figs. 4, 5, SM) and by slightly-narrowed median region in the male palpal bulb (Figs. 3, 4, 19, 20). The females differ by the bulb-like shape of the anterior pair of seminal receptacles very close to the posterior pair (Fig. 22).

Male.—(Parque Nacional da Serra do Divisor, IBSP 12305). Carapace yellow with light brown spotted pattern as shown in Fig. 18. Pedipalps light yellow with brownish stains. Labium and endites cream colored with brownish margins. Sternum as in *S. championi* but cream colored. Legs light yellow with scattered brown spots except on tarsi. Abdomen grayish. Total length 4.50. Carapace slightly domed, 2.13 long, 1.76 wide. Eye diameters: PME 0.18, ALE 0.16, PLE 0.16. Lateral eyes and chelicerae as in *S. championi.* Labium 0.16 long, 0.22 wide. Sternum 0.88 long, 1.13 wide. Leg measurements: I - femur 10.00/ patella 0.63/ tibia 10.50/ metatarsus 15.00/ tarsus 0.88/ total 37.01/ II - 6.50/ 0.63/ 6.50/ 8.00/ 0.75/ 22.38/ III - 3.63/ 0.63/ 3.38/ 3.88/ 0.63/ 12.15/ IV - 6.00/ 0.63/ 5.75/ 6.88/ 0.75/ 20.01. Palpal femur presenting stridulatory pick long and slender with oval and projected socket (Fig. 6). Cymbium presenting single distal slender spine (Fig. 19). Bulb 0.70 long. Distal area ventrally with anterior serrated membrane followed by small triangular pocket (P; Figs. 4, 5, 20). Abdomen 2.38 long,

1.30 wide, rounded, covered with slender hairs.

Female.—(Parque Nacional da Serra do Divisor, IBSP 12526). Coloration as in male. Total length 5.13. Carapace slightly domed, 2.38 long, 1.88 wide. Eye diameters: PME 0.14, ALE 0.14, PLE 0.16. Lateral eyes and chelicerae as in male. Labium 0.32 long, 0.26 wide. Sternum 1.20 long, 0.94 wide. Leg measurements: I - femur 6.25/ patella 0.63/ tibia 7.13/ metatarsus 4.25/ tarsus 0.75/ total 19.01/ II - 4.38/ 0.63/ 4.13/ 4.50/ 0.75/ 19.01/ III - 2.75/ 0.50/ 2.63/ 2.88/ 0.63/ 9.39/ IV - 4.38/ 0.63/ 4.25/ 4.88/ 0.75/ 14.89. Epigynal fovea narrow, curved and parallel, widely separated. Positioning ridge semicircular (Fig. 21). Internal genitalia with two pairs of seminal receptacles with short ducts. Central pair with strongly sclerotized ring at base (Fig. 22). Abdomen 2.88 long, 1.75 wide, as in male.

Variation.—Carapace pattern varies greatly as shown in Fig. 18, 23–25. *Males:* Total length 3.50–4.88; carapace 1.63–2.38; femur I 5.63–11.38; bulb 0.38–0.64 ($n = 10$). *Females:* Total length 3.50–6.00; carapace 1.50–3.63; femur I 4.13–7.00 ($n = 15$). Genitalic morphology constant.

Distribution.—North and northeastern Brazil.

Material examined.—BRAZIL: *Acre:* Parque Nacional da Serra do Divisor, 1♀, 13 November 1996, R.S. Vieira (IBSP 9137); 3♀, 9 November 1996, R.S. Vieira (IBSP 8971); 2♀, 5–25 November 1996, R.S. Vieira (IBSP 9268); (Tipologia 9, sítio 10), 1♀, 23 March 1997, L. Resende & R.S. Vieira (IBSP 12426); (Anil), 2♂, 10 November 1996, R.S. Vieira (IBSP 9494); (Tipologia 9, sítio 11), 2♀, 25 March 1997, L. Resende & R.S. Vieira (IBSP 12179); (Várzea Gibralta-Pedro), 1♂, 20 November 1996, R.S. Vieira (IBSP 9355); (Tipologia 7, sítio 4), 2♀, 15 March 1997, L. Resende & R.S. Vieira (IBSP 12379); (Travessa Baixa), 1♂1♀, 16 November 1996, R.S. Vieira (IBSP 9407); (Tabocão), 1♂1♀, 17 November 1996, R.S. Vieira (IBSP 9188); (Tipologia 8, sítio 1), 3♂, 10 March 1997, L. Resende & R.S. Vieira (IBSP 12466); (Juazeiro), 1♀, 23 November 1996, R.S. Vieira (IBSP 9012); (Tipologia 8, sítio 4), 1♂, 14 March 1997, L. Resende & R.S. Vieira (IBSP 12305); (Tipologia 7, sítio 4), 3♂2♀, 18 March 1997, L. Resende & R.S. Vieira (IBSP 12526); Rio Branco (Reserva Extrativista de Humaitá), 1♂, 12 April 1996, Eq. IBSP/ SMNK (IBSP 8748); *Amazonas:* Manaus (Igapó, Tarumã-Mirim), 1♀, 5 February 1988, H. Höfer (SMNK 271); 1♂, 2 December 1987, H. Höfer
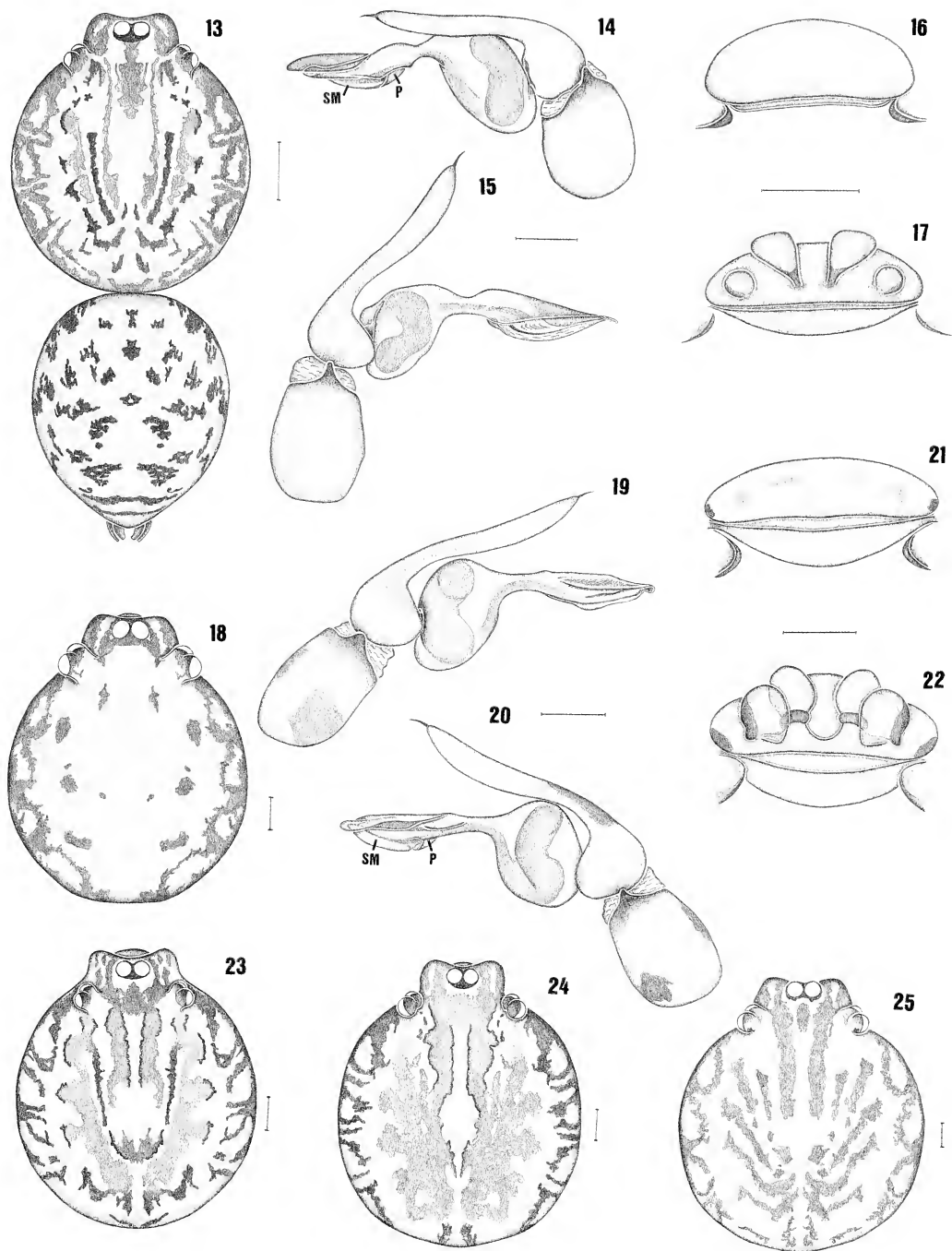
Figures 13–25.—13–17. *Scytodes championi* F.O.P.-Cambridge. 13. Male body, dorsal view; 14. Male palp, retrolateral view; 15. Prolateral view; 16. Female epigynum, ventral view; 17. Dorsal view. 18–25. *Scytodes romitii* Caporiacco. 18. Male carapace, dorsal view; 19. Male palp, prolateral view; 20. Retrolateral view; 21. Female epigynum, ventral view; 22. Dorsal view. 23–25. Male carapace, dorsal view, variation patterns: 23. São Mateus, Espirito Santo; 24. Serra do Teimoso, Jussari, Bahia; 25. Tefé, Amazonas. Scale lines = 0.25 mm.

(SMNK 272); 1 juv., 17 February 1988, H. Höfer (SMNK); 1♂, 8 October 1987, H. Höfer (SMNK); 1♂1♀, 2 December 1987, H. Höfer (SMNK); 1♂, 3 October 1987, H. Höfer (SMNK); 1♀, 1 February 1983, H. Höfer (SMNK); (Ilha da Marchantaria); 19 January 1988, H. Höfer (SMNK 946); (Fazenda Esteio ZF3-Km 23), 1♂, 25 February 1987, B.C. Klein (INPA); 1♀, 7 November 1985, B.C. Klein (INPA); 1♂, 5 May 1985, B.C. Klein (INPA); Alto Solimões, 1♀, 1 juv., December 1997, A.A. Lise (MCN 8894); Tefé (Estação Ecológica do Mamirauá), 1♂1♀, 9–13 October 1992, S.H. Borges (MCN 22876); *Rondônia:* Porto Velho, 1♀, 15 April 1996, Eq. IBSP/SMNK (IBSP 8711); *Bahia:* 2♂3♀, Ceplac (MNRJ); Camacan (Fazenda Matiapã), 2♀, 2 juvs., 16 October 1978, J.S. Santos (CEPLAC); 1♀, 16 October 1978, J.S. Santos (CEPLAC); 1♀, 16 October 1978, J.S. Santos (CEPLAC); Itamarajú, 1♀, Ceplac (MNRJ); (Fazenda Nossa Senhora das Neves); 3♂2♀, 14 October 1978, J.S. Santos (CEPLAC); (Fazenda Pau Brasil), 1♂, 22 December 1969, Ceplac (MNRJ 13354); 1♂3♀, 20 June 1968, Ceplac (MNRJ 13388); Juçari 1♀, Ceplac (MNRJ); (Fazenda Arizona), 1♂, 4 March 1971, Ceplac (MNRJ); (Fazenda Ribeirão do Antônio), 1♀, 1 juv., 13 May 1970, Ceplac (MNRJ); (Fazenda São Francisco), 1♀, 26 November 1970, Ceplac (MNRJ); 3♀, 27 November 1969, Ceplac (MNRJ); 2♂, 27 November 1969, Ceplac (MNRJ 13345); 1♂, 24 September 1970, Ceplac (MNRJ 13062); 1♀, 8–9 April 1998, A.D. Brescovit et al. (IBSP 18576); (Fazenda Bethania), 2♀, 1 juv., 17 April 1971, Ceplac (MNRJ); Uruçuca, 1♂, 2 juvs., Ceplac (MNRJ 13381); (Fazenda Santa Tereza), 1♀, 21 October 1970, Ceplac (MNRJ); Juçari, Reserva Natural da Serra do Teimoso, 1♀, April 1998, A.D. Brescovit & R. Bertani (IBSP 18825); Ilhéus (Ceplac), 1♀, 12 April 1998, A.D. Brescovit et al. (IBSP 18909); Lomanto Junior (Fazenda Mangabeira), 4♂, 29 May 1968, Ceplac (MNRJ); Mascote (Fazenda Palestina), 2♂, 11 May 1968, Ceplac (MNRJ); 7♂1♀, 11 May 1968, Ceplac (MNRJ); Porto Seguro (Fazenda São Jorge), 1♀, 28 June 1970, Ceplac (MNRJ); Coaraci (Fazenda Boa Esperança), 1♂, 24 March 1971, Ceplac (MNRJ); 1♀, 18 September 1970, Ceplac (MNRJ); 1♀, 3 November 1970, Ceplac (MNRJ); 2♀, 17 October 1970, Ceplac (MNRJ); 3♂3♀, 28 January 1971, Ceplac (MNRJ); 1♀, 16 January 1971, Ceplac (MNRJ); Mascote (Fazenda Palestina), 10♂, 9 June 1968, Ceplac (MNRJ); Gandu (Fazenda Pedra Branca), 1♂, 5 February 1970, Ceplac (MNRJ); Prado (Fazenda Furado), 1♂, 26 September 1970, Ceplac (MNRJ); Espírito Santo: São Mateus (Reserva Florestal Vale do Rio Doce), 1♀, 5–12 January 1998, A.D. Brescovit et al. (IBSP 16955); 1♀, 5–12 January 1998, A.D. Brescovit et al. (IBSP 16758); 1♂, 4 juv., 5–12 January 1998, A.D. Bres-

covit et al. (IBSP 21429); 1♀, 7 juv., 5–12 January 1998, A.D. Brescovit et al. (IBSP 21436).

Scytodes panamensis new species
(Figs. 7, 8, 26–30)

Types.—Male holotype from Fort Sherman, Canal Zone, Panama, 15 August 1939, A.M. Chickering deposited in MCZ. Six male and 15 female paratypes deposited in MCZ and two male and three female paratypes deposited in IBSP 24029, all with the same data as holotype.

Etymology.—The specific name refers to the type locality.

Diagnosis.—The males of *S. panamensis* differ from the other species, here included, by the dorsal rectangular hump on the male palpal bulb (Figs. 8, 27). The female differs from the other species by the transversal pair of oval seminal receptacles (Fig. 30).

Male.—(Portobelo, Canal Zone, Panama). Carapace yellow with U-shaped dark brown pattern as shown in Fig. 26. Pedipalps yellow with brown longitudinal dorsal stripe and one or two scattered brown stains. Labium and endites yellow. Sternum cream colored with brown margins at base of legs and along slight grooves that extend towards center. Legs yellow with pair of brown longitudinal ventral stripes along femur and single brown longitudinal dorsal stripe along tibia and metatarsus. Abdomen grayish with two or three posterior longitudinal black stripes and few anterior scattered black stains (Fig. 30). Total length 4.50. Carapace slightly domed, 2.25 long, 1.88 wide. Eye diameters: PME 0.14, ALE 0.14, PLE 0.14. Lateral eyes and chelicerae as in *S. championi.* Labium 0.24 long, 0.28 wide. Sternum 1.24 long, 0.92 wide. Leg measurements: I - femur 5.13/ patella 0.63/ tibia 5.63/ metatarsus 7.38/ tarsus 0.88/ total 19.65/ II - 3.63/ 0.63/ 4.00/ 4.38/ 0.75/ 13.39/ III - 2.50/ 0.50/ 2.13/ 2.63/ 0.63/ 8.39/ IV - 3.63/ 0.63/ 3.38/ 3.75/ 0.75/ 12.14. Palpal femur as in *S. championi.* Cymbium with single distal spine (Fig. 27). Bulb 0.56 long, distal area with ventral spoon-shaped, slightly sclerotized pocket (P, Fig. 27). Abdomen 2.25 long, 1.38 wide, rounded, covered with slender hairs.

Female.—(Portobelo, Canal Zone, Panama). Coloration as in male. Total length 4.75. Carapace slightly domed, 2.38 long, 2.00 wide. Eye diameters: PME 0.14, ALE 0.14,
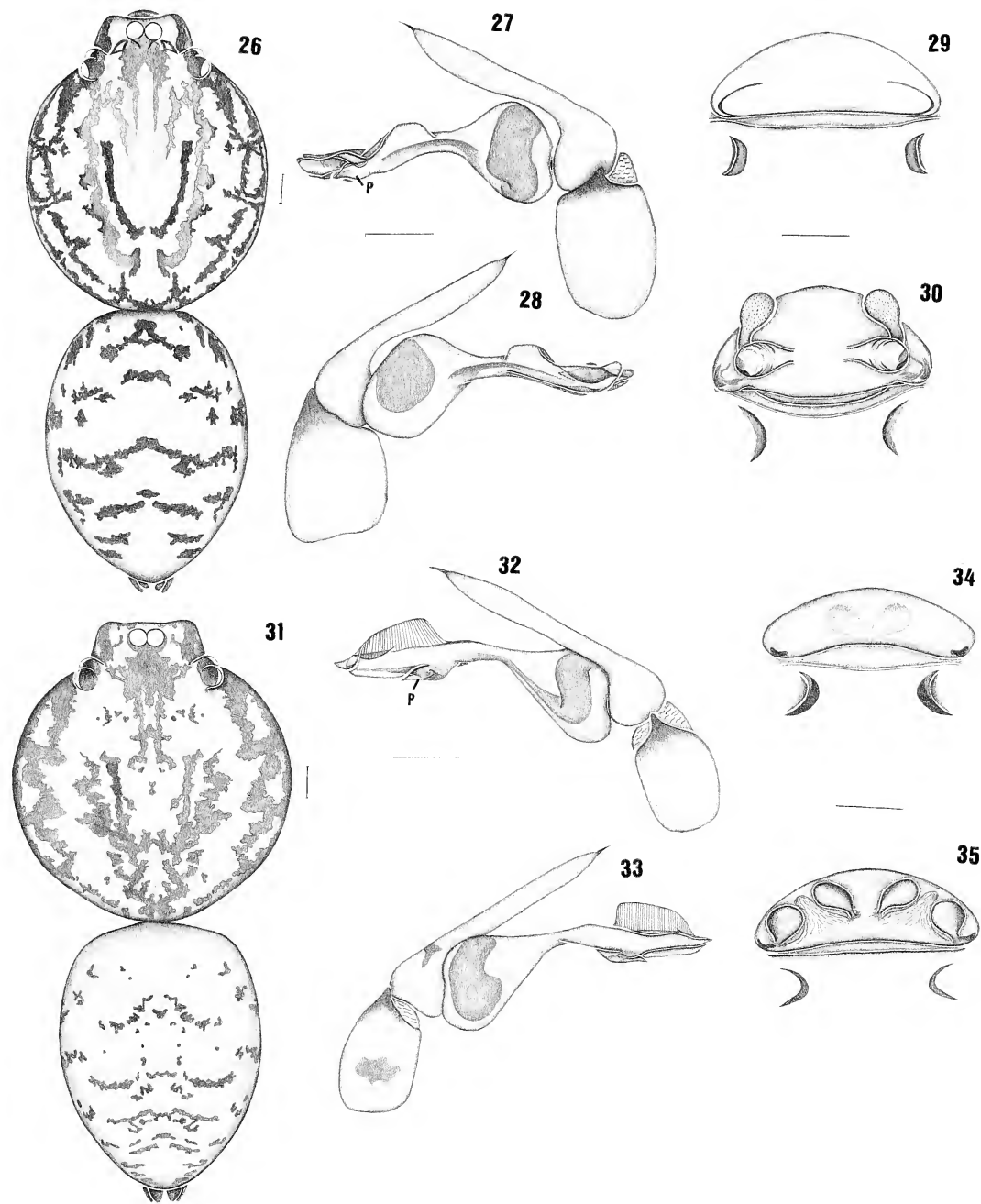
Figures 26–35.—26–30. **Scytodes panamensis** new species. 26. Male body, dorsal view; 27. Male palp, retrolateral view; 28. Prolateral view; 29. Female epigynum, ventral view; 30. Dorsal view. 31–35, *Scytodes guttipes* Simon. 31. Male body, dorsal view; 32. Male palp, retrolateral view; 33. Prolateral view; 34. Female epigynum, ventral view; 35. Dorsal view. Scale lines = 0.25 mm.

PLE 0.16. Lateral eyes and chelicerae as in male. Labium 0.30 long, 0.36 wide. Sternum 1.32 long, 0.96 wide. Leg measurements: I - femur 3.00/ patella 0.50/ tibia 3.00/ metatarsus 3.75/ tarsus 0.50/ total 10.75/ II - 2.25/ 0.50/ 2.38/ 2.63/ 0.63/ 8.39/ III - 1.63/ 0.38/ 1.50/ 1.75/ 0.50/ 5.76/ IV - 2.25/ 0.63/ 2.38/ 2.38/ 0.50/ 8.14. Epigynal fovea semicircular, wide-

ly separated from each other. Positioning ridge semicircular (Fig. 29). Internal genitalia presenting posterior pair of seminal receptacles with long ducts (Fig. 30). Abdomen 2.38 long, 2.25 wide, as in male.

Variation.—*Males:* Total length 3.63–5.75; carapace 2.00–2.75; femur I 4.13–6.50; bulb 0.48–0.68 (*n* = 15.) *Females:* Total length 4.25–5.75; carapace 2.38–2.88; femur I 2.50–3.88 (*n* = 20). Some males with a single row of spines along the ventral face of the tibia I. Genitalic morphology constant.

Distribution.—Canal Zone, Panama.

Material examined.—PANAMA: *Canal Zone:* Gatun, 1♀, 11 juvs., 15 February 1958, A.M. Chickering (MCZ); Fort Sherman, 7♂11♀, August 1939, A.M. Chickering (MCZ); Fort Gulik, 2♂, September 1979, H.J. Harlan (AMNH); Portobelo, 9♂18♀, 10 juvs., 12 August 1936, A.M. Chickering (MCZ).

Scytodes guttipes Simon
(Figs. 31–35)

Scytodes guttipes Simon 1892: 438, pl. 9, fig. 13 (3♂, 1♀, 5 immature syntypes from Venezuela, with no definite locality, deposited in MNHN AR1223, examined. Lectotype ♂ and 2♂, ♀ and 5 immature paralectotypes hereby designated). Roewer, 1942: 329.

Diagnosis.—*Scytodes guttipes* differs from the other species by the presence of a developed dorsal membrane in the distal area of the male palpal bulb (Figs. 32–33) and by the slightly sclerotized projection between the female seminal receptacles (Fig. 35).

Male.—(Lectotype). Carapace yellow with dark pattern as shown in Fig. 31. Labium and endites yellow with brownish margins. Pedipalps, sternum and legs yellow with black stains. Abdomen cream colored with few black transversal scattered stains. Total length 4.50. Carapace, 2.25 long, 1.75 wide. Eye diameters: PME 0.10, ALE 0.12, PLE 0.12. Lateral eyes and chelicerae as in *S. championi*. Labium 0.26 long, 0.20 wide. Sternum 1.14 long, 0.74 wide. Leg measurements: I - femur 6.88/ patella 0.63/ tibia 7.00/ metatarsus 9.00/ tarsus 0.75/ total 24.26/ II - 4.50/ 0.50/ 4.50/ 5.25/ 0.63/ 15.38/ III - 3.00/ 0.50/ 2.50/ 3.38/ 0.63/ 10.01/ IV - 4.25/ 0.50/ 4.13/ 4.63/ 0.75/ 14.26. Palpal femur as *S. championi*. Cymbium with strong distal spine (Fig. 32). Bulb 0.54 long, medially narrowed (Fig. 33). Distal

area with median ventral lance-shaped pocket (P; Fig. 32). Abdomen 2.25 long, 1.75 wide, rounded, covered with slender hairs.

Female.—(Paralectotype). Coloration as in male. Total length 4.88. Carapace 2.50 long, 2.13 wide. Eye diameters PME 0.12, ALE 0.12, PLE 0.14. Lateral eyes and chelicerae as in male. Labium 0.32 long, 0.30 wide. Sternum 1.38 long, 1.00 wide. Leg measurements: I - femur 4.38/ patella 0.63/ tibia 4.25/ metatarsus 5.63/ tarsus 0.75/ total 15.64/ II - 3.50/ 0.50/ 3.13/ 3.88/ 0.63/ 11.64/ III - 2.13/ 0.50/ 1.75/ 2.38/ 0.50/ 7.26/ IV - 2.75/ 0.50/ 2.50/ 3.25/ 0.75/ 9.75. Epigynal fovea narrow and semicircular. Positioning ridge semicircular (Fig. 34). Internal genitalia with two pairs of oval seminal receptacles (Fig. 35). Abdomen 2.38 long, 2.25 wide, as in male.

Variation.—*Males:* Total length 3.88–4.50; carapace 2.13–2.25; femur I 4.88–6.88 (*n* = 2).

Distribution.—Venezuela and Trinidad & Tobago.

Other material examined.—TRINIDAD & TOBAGO: Mount St. Benedict (10°39′49″N, 61°23′56″W), 1♂, 27–30 June 1999, R. Pinto-da-Rocha (MZSP 18880).

Scytodes cogu new species
(Figs. 36–40)

Scytodes championi: Valerio 1981: 86–87 (Misidentification, only figs. 17 and 29).

Types.—Male holotype, 5♀ and 5 immature paratypes from San José, San José Province, Costa Rica, E. Schmidt, deposited in AMNH; and 2♀ paratypes, with the same data, deposited in IBSP 24026.

Etymology.—Short for "cogumelo." Brazilian word for mushroom, due to the shape of one pair of seminal receptacles.

Diagnosis.—The male of *Scytodes cogu* resembles *S. vaurieorum* by the pronounced groove with lateral projections in the apex of the distal area of the male palpal bulb (Figs. 37, 50) but differs by the presence of short and narrowed median ventral projection and absence of slightly sclerotized membrane (Fig. 38). The females differ from the other species by the presence of a pair of anterior mushroom-like seminal receptacles and a pair of posterior curved truncated ones (Fig. 40).

Male.—(Holotype). Carapace light brown with brown pattern as shown on Fig. 36. Ped-
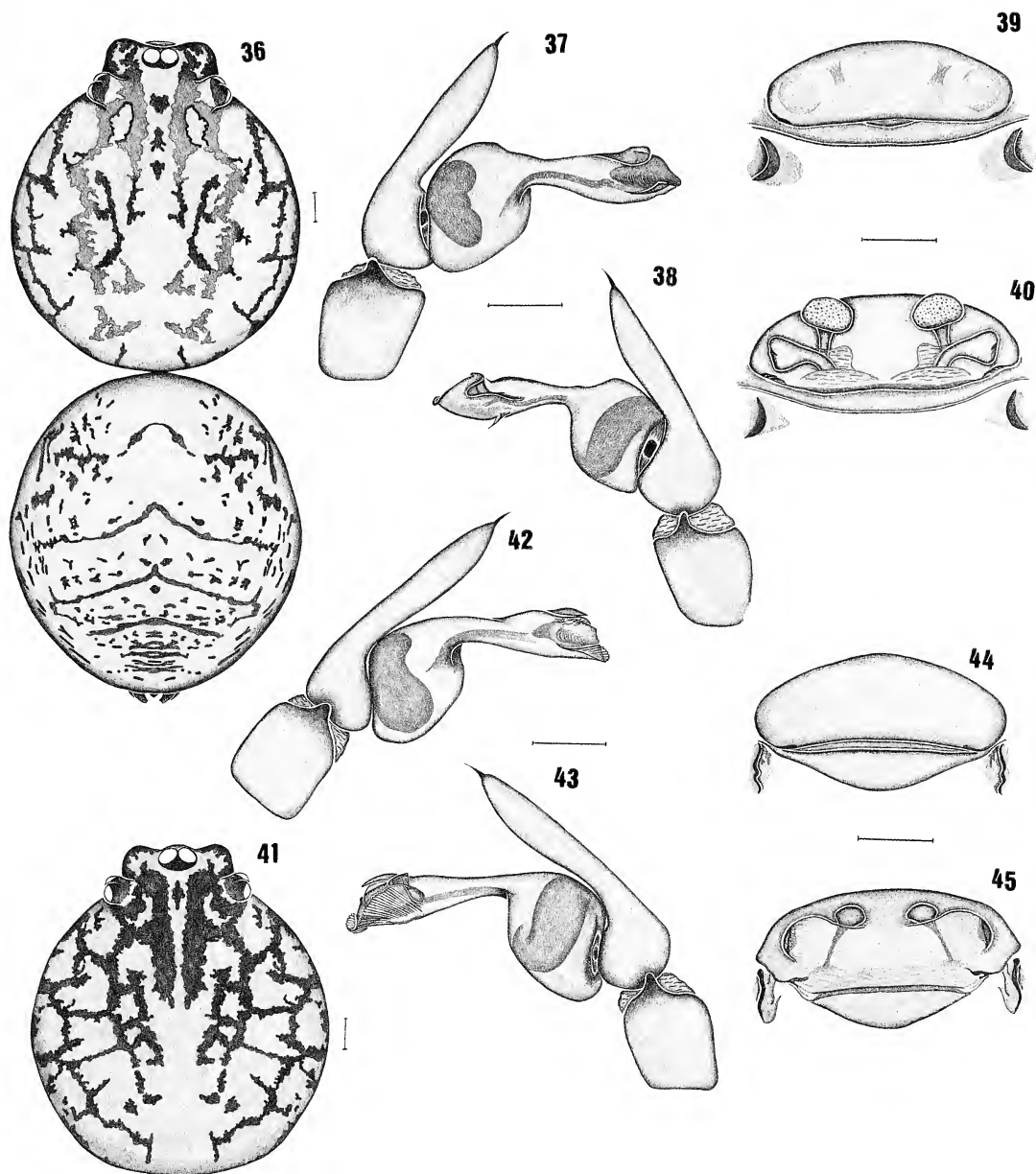
Figures 36–45.—36–40. **Scytodes cogu** new species. 36. Male body, dorsal view; 37. Male palp, prolateral view; 38. Retrolateral view; 39. Female epigynum, ventral view; 40. Dorsal view. 41–45. **Scytodes vaurieorum** new species. 41. Male carapace, dorsal view; 42. Male palp, prolateral view; 43. Retrolateral view; 44. Female epigynum, ventral view; 45. Dorsal view. Scale lines = 0.25 mm.

ipalps yellow with dorsal longitudinal stripe. Labium and endites yellow. Sternum yellow with brown margins at base of legs and along slight grooves extending towards center. Legs yellow with scattered longitudinal stains. Abdomen grayish with black pattern of transversal stripes with few scattered black spots be-

tween them and lateral black stains (Fig. 36). Total length 4.25. Carapace 2.00 long, 1.63 wide. Eye diameters: PME 0.14, ALE 0.14, PLE 0.14. Lateral eyes and chelicerae as in *S. championi*. Labium 0.18 long, 0.28 wide. Sternum 1.20 long, 0.94 wide. Leg measurements: I - femur 3.00/ rest of leg absent/ II -

femur 2.75/ patella 0.63/ tibia 2.88/ metatarsus 3.63/ tarsus 0.63/ total 10.52/ III - 1.75/ 0.50/ 1.63/ 2.00/ 0.63/ 6.51/ IV - 2.63/ 0.63/ absent/ absent. Palpal femur as in *S. championi*. Cymbium with slender distal spine (Fig. 37). Bulb 0.54 long, distal area with dorsal, sclerotized membrane (Fig. 37). Abdomen 2.25 long, 1.38 wide, rounded, covered with slender hairs.

Female.—(Paratype). Coloration as in male. Total length 4.38. Carapace 2.13 long, 1.75 wide. Eye diameters: PME 0.14, ALE 0.12, PLE 0.14. Lateral eyes and chelicerae as in male. Labium 0.20 long, 0.24 wide. Sternum 1.12 long, 0.92 wide. Leg measurements: I - femur 2.13/ patella 0.50/ tibia 2.38/ metatarsus 2.88/ tarsus 0.63/ total 8.52/ II - 1.88/ 0.50/ 1.88/ 2.00/ 0.50/ 6.76/ III - 1.38/ 0.38/ 1.13/ 1.13/ 0.50/ 4.52/ IV - 2.00/ 0.50/ 1.75/ 1.88/ 0.63/ 6.73. Epigynal fovea semicircular, shalow. Positioning ridge semicircular (Fig. 39). Abdomen 2.25 long, 2.25 wide, as in male.

Variation.—*Females:* Total length 4.25–5.00; carapace 2.13–2.75; femur I 2.13–2.75 (*n* = 7).

Distribution.—Costa Rica.

Material examined.—COSTA RICA: Three minutes south Liberia, Guanacaste Province, 1♀, 10 July 1966, S. Peck (AMNH).

Scytodes vaurieorum new species
(Figs. 41–45)

Types.—Male holotype from San Jeronimo Department, Guatemala, 24–26 July 1947, C. & P. Vaurie; and female paratype from the same locality, 26–27 July 1947, C. & P. Vaurie deposited in AMNH.

Etymology.—The specific name is a patronym in honor of the collectors of the types.

Diagnosis.—*Scytodes vaurieorum* differs from *S. cogu* by the presence of a slightly sclerotized membrane located all around the distal area and by a finger-like dorsal projection (Fig. 43). The female differs from the other species by the presence of a sinuous positioning ridge (Fig. 44) and by a pair of small seminal receptacles with long ducts (Fig. 45).

Male. (Holotype).—Carapace light brown with brown pattern as shown on Fig. 41. Pedipalps light brown with few ventral spots. Labium and endites yellow with brownish margins. Sternum yellow with brown margins at base of legs and along slight groves extending towards center. Legs yellowish with many ventral scattered black spots, except on tarsi. Abdomen grayish. Total length 4.13. Carapace slightly domed, 2.13 long, 1.88 wide. Eye diameters: PME 0.12, ALE 0.10, PLE 0.12. Lateral eyes and chelicerae as in *S. championi*. Labium 0.14 long, 0.24 wide. Sternum 1.18 long, 0.88 wide. Leg measurements: I - femur 2.63/ patella 0.50/ tibia 3.13/ metatarsus 3.75/ tarsus 0.63/ total 10.64/ II - 2.13/ 0.50/ 2.13/ 2.38/ 0.63/ 5.88/ III - 1.50/ 0.50/ 1.25/ 1.50/ 0.50/ 5.25/ IV - 2.13/ 0.50/ 2.13/ 2.13/ 0.63/ 7.52. Palpal femur as in *S. championi*. Cymbium with single apical slender spine (Fig. 42). Bulb 0.52 long, strongly curved inwards with distal area presenting prolateral concavity (Fig. 42). Abdomen 2.00 long, 1.75 wide, rounded, covered with slender hairs.

Female. (Paratype).—Coloration as in male. Total length 4.63 Carapace slightly domed, 2.13 long, 1.88 wide. Eye diameters: PME 0.14, ALE 0.12, PLE 0.12. Lateral eyes and chelicerae as in male. Labium 0.24 long, 0.24 wide. Sternum 1.18 long, 0.90 wide. Leg measurements: I - femur 2.25/ patella 0.50/ tibia 2.38/ metatarsus 2.75/ tarsus 0.63/ total 8.51/ II - 1.75/ 0.50/ 1.75/ 2.13/ 0.50/ 6.63/ III - 1.25/ 0.50/ 1.13/ 1.00/ 0.38/ 4.26/ IV - 1.75/ 0.50/ 1.75/ 1.75/ 0.63/ 6.38. Epigynal fovea inconspicuous (Fig.44). Internal genitalia with pair of seminal receptacles on each side. Larger globose pair covering ducts of smaller pair and with lateral sclerotized area (Fig. 45). Abdomen 2.50 long, 2.25 wide, as in male.

Distribution.—Known only from the type locality.

Material examined.—Only the types.

Scytodes tegucigalpa new species
(Figs. 9, 10, 46–48)

Types.—Male holotype from Tegucigalpa, Francisco Morazán Department, Honduras, November 1959, N.H.L. Krauss, deposited in AMNH. 1♂ (IBSP 24027) and 1♂ and 3 immature (AMNH) paratypes from same locality as holotype, 14 July 1948, Clark.

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—The male of *S. tegucigalpa* resembles *S. chiquimula* by the presence of an apical projection on the bulb (Figs. 50, 51) but differs by the presence of bifid distal area and dorsal groove (Figs. 10, 47, 48).
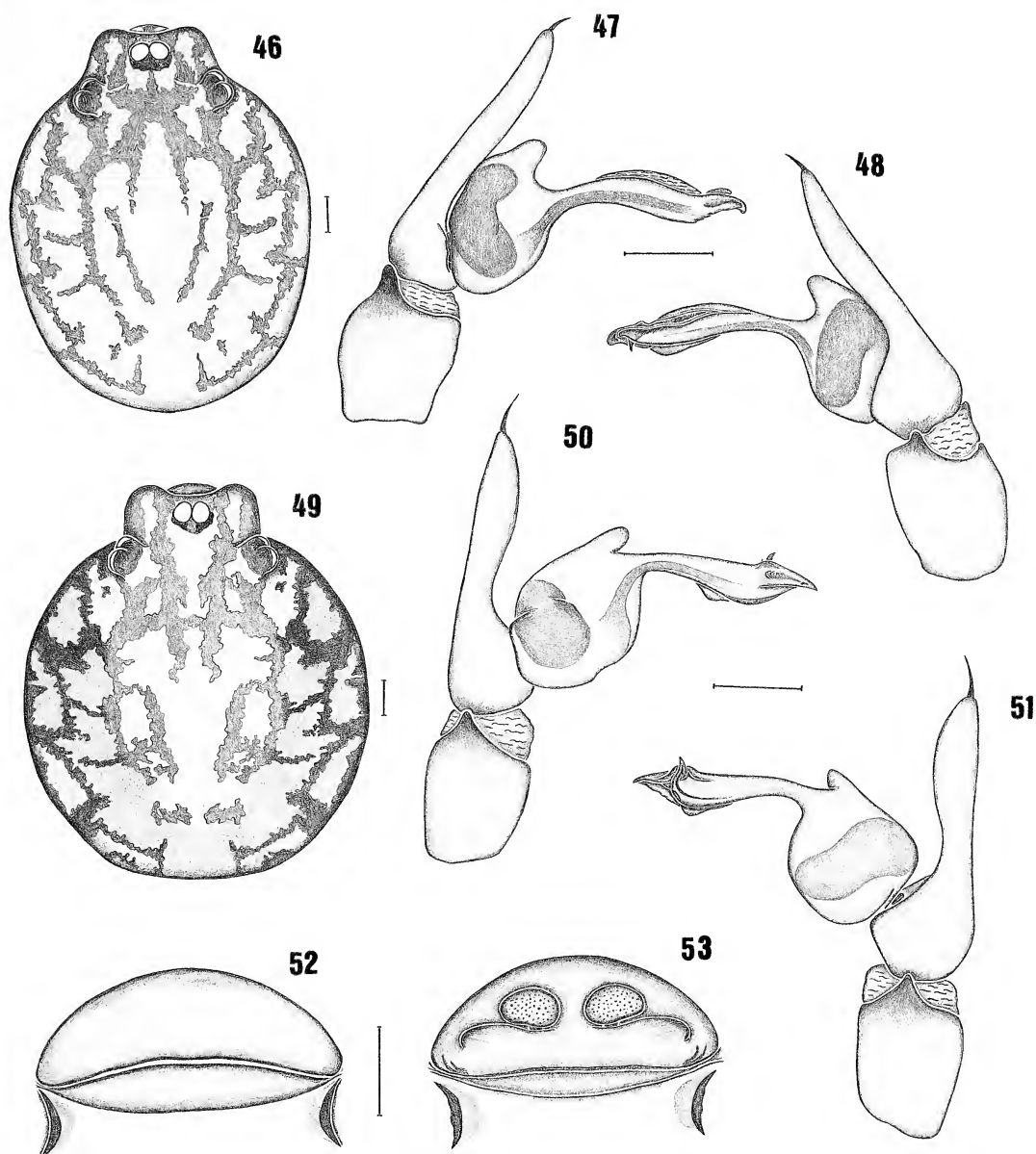
Figures 46–53.—46–48. **Scytodes tegucigalpa** new species. 46. Male carapace, dorsal view; 47. Male palp, prolateral view; 48. Retrolateral view. 49–53. **Scytodes chiquimula** new species. 49. Male carapace, dorsal view; 50. Male palp, prolateral view; 51. Retrolateral view; 52. Female epigynum, ventral view; 53. Dorsal view. Scale lines = 0.25 mm.

Male. (Holotype).—Carapace yellow with brown pattern as shown in Fig. 46. Pedipalps yellow. Labium and endites yellow. Sternum yellow with brown margins at base of legs and along slight grooves extending toward center. Legs yellow with pair of ventral longitudinal stripes along femora and few scattered longitudinal stains along tibiae. Abdomen grayish. Total length 4.63. Carapace slightly domed, 2.25 long, 1.88 wide. Eye diameters: PME 0.12, ALE 0.12, PLE 0.14. Lateral eyes and chelicerae as in *S. championi*. Labium 0.28 long, 0.24 wide. Sternum 1.34 long, 0.98 wide. Leg measurements: I - femur 4.25/ patella 0.50/ tibia 5.00/ metatarsus 6.13/ tarsus 0.75/ total 16.63/ II - 3.00/ 0.50/ 3.25/ 3.75/

0.75/ 11.25/ III - 2.13/ 0.50/ 1.88/ 2.13/ 0.75/ 7.39/ IV - 3.00/ 0.63/ 2.88/ 3.13/ 0.75/ 10.39. Palpal femur as in *S. championi*. Cymbium with single slender distal spine (Fig. 47). Bulb 0.56 long, distal area with slightly sclerotized dorsal membrane (Figs. 10, 47) and a short ventral triangular projection (Fig. 48). Abdomen 2.38 long, 2.00 wide, rounded, covered with slender hairs.

Female.—Unknown.

Variation.—*Males:* Total length 4.63–5.00; carapace 2.25–2.75; femur I 4.25–5.88; bulb 0.56–0.64 ($n = 3$).

Distribution.—Known only from the type locality.

Material examined.—Only the types.

Scytodes chiquimula new species
(Figs. 49-53)

Types.—Male holotype, 1♀ and 1 immature paratype from Chiquimula (1250 ft.), Chiquimula Department, Guatemala, 21–23 July 1947, C. & P. Vaurie, deposited in AMNH, and female paratype, with the same data as holotype, deposited in IBSP 24028.

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—The male of *S. chiquimula* differs from *S. tegucigalpa* by the presence of a retrolateral curved lamina apically projected (Fig. 51) and by a distal triangular laminar projection (Fig. 50) on the distal area of palpal bulb. The female resembles *S. cogu* by a pair of anterior mushroom-like seminal receptacles but differs by the short ducts and the elliptical posterior pair (Fig. 53).

Male. (Holotype).—Carapace light brown with brown pattern as shown on Fig. 49. Pedipalps yellow. Labium and endites yellow. Sternum yellow with brown margins at the base of each leg. Legs yellowish with many black small ventral longitudinal stains. Abdomen grayish. Total length 4.88 Carapace slightly domed, 2.63 long, 2.00 wide. Eye diameters: PME 0.14, ALE 0.14, PLE 0.14. Lateral eyes and chelicerae as in *S. championi*. Labium 0.28 long, 0.30 wide. Sternum 1.40 long, 1.00 wide. Leg measurements: I - femur 4.00/ patella 0.63/ tibia 4.63/ metatarsus 5.63/ tarsus 0.75/ total 15.64/ II - 3.00/ 0.50/ 3.13/ 3.75/ 0.63/ 11.01/ III - 2.13/ 0.50/ 1.75/ 2.25/ 0.63/ 7.26/ IV - 3.00/ 0.63/ 3.13/ 2.88/ 0.63/ 10.27. Palpal femur with stridulatory pick

short and strong with rounded and projected socket. Cymbium with single slender apical spine (Fig. 50). Bulb 0.60 long. Abdomen 2.25 long, 1.63 wide, rounded, covered with slender hairs.

Female. (Paratype, AMNH).—Coloration as in male. Total length 3.88. Carapace domed, 2.38 long, 2.13 wide. Eye diameters: PME 0.12, ALE 0.12, PLE 0.12. Lateral eyes and chelicerae as in male. Labium 0.20 long, 0.22 wide. Sternum 1.26 long, 0.88 wide. Leg measurements: I - femur 3.13/ patella 0.63/ tibia 2.88/ metatarsus 4.00/ tarsus 0.75/ total 11.39/ II – 2.75/ 0.63/ 2.38/ 2.88/ 0.63/ 9.27/ III – 1.88/ 0.63/ 1.50/ 1.88/ 0.63/ 6.52/ IV – 2.63/ 0.63/ 2.63/ 2.75/ 0.75/ 9.39. Fovea inconspicuous. Positioning ridge semicircular (Fig. 52). Abdomen 1.50 long, 1.75 wide, as in male.

Variation.—Females: total length 3.88–5.25; carapace 2.38–2.63; femur I 2.50–3.13 ($n = 2$).

Distribution.—Known only from the type locality.

Material examined.—Only the types.

Scytodes zamorano new species
(Figs. 54–56)

Scytodes championi: Valerio 1981: 86 (misidentification, only fig. 18).

Types.—Female holotype and female paratype from Zamorano, El Paraiso Department, Honduras, September 1953, N.H.L. Krauss deposited in AMNH.

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—The female of *S. zamorano* differs from the other species herein included by the sac-like positioning ridge (Figs. 55, 56).

Male.—Unknown.

Female (paratype).—Carapace yellow with brown pattern (Fig. 54). Pedipalps yellow with longitudinal brown stains. Labium and endites yellow. Sternum yellow with brown margins at base of legs extending towards center along slight grooves. Legs yellow with pair of brown longitudinal stripes along ventral face of femora and few scattered longitudinal stains along tibiae. Abdomen uniformly gray. Total length 5.25. Carapace slightly domed, 2.75 long, 2.00 wide. Eye diameters: PME 0.14, ALE 0.14, PLE 0.14. Lateral eyes

and chelicerae as in *S. championi.* Labium 0.28 long, 0.32 wide. Sternum 1.42 long, 1.08 wide. Leg measurements: I - femur 2.88/ patella 0.63/ tibia 3.13/ metatarsus 3.75/ tarsus absent/ total 10.39/ II – 2.25/ 0.50/ 2.38/ 2.75/ 0.75/ 8.63/ III – 1.63/ 0.50/ 1.50/ 1.75/ 0.63/ 6.01/ IV – 2.25/ 0.63/ 2.38/ 2.38/ 0.75/ 8.39. Epigynal fovea very deep (Fig. 55). Internal genitalia with pair of anterior globose seminal receptacles and pair of posterior oval seminal receptacles with slender, strongly curved ducts (Fig. 56). Abdomen 2.50 long, 2.13 wide, rounded, covered with slender hairs.

Variation.—*Females:* Total length 5.00–5.25; carapace 2.50–2.75; femur I 2.88–3.13 (*n* = 2).

Distribution.—Known only for the type locality.

Material examined.—Only the types.

Scytodes armata new species
(Figs. 11, 12, 57–61)

Scytodes championi: Valerio 1981: 87 (misidentification, only fig. 28).

Types.—Male holotype from La Selva, Puerto Viejo, Heredia, Costa Rica, December 1980, W. Eberhard; 1♂ paratype from same locality, February 1981, W. Eberhard; 1♂ paratype from Cahuita, Limon, Costa Rica, 30 March 1979, J. Coddington; and 3♀ and 1 immature paratypes from Monteverde Community, Puntarenas, Costa Rica, July 1978, C.L. Kraig & P. Klass, all deposited in MCZ.

Etymology.—The specific name refers to the strong ventral spines along male legs I and II.

Diagnosis.—The males of *Scytodes armata* resemble those of *S. univittata* Simon 1882 (see Brescovit & Rheims 2000, fig. 16) by the double row of spines along ventral face of the femur I but differ by a double row of spines also along femur II (Fig. 12). It differs from the other species, as well as *S. univittata* by the presence of a tubular retrolateral projection on the distal area of the male palpal bulb (Fig. 58). The females resemble those of *S. gertschi* by the pair of anterior, rounded, mushroom-like seminal receptacles but differ by straight posterior area of epigynal plate (Fig. 60) and rounded shape of anterior pair of seminal receptacles (Fig. 61).

Male (holotype).—Carapace yellow with brown pattern (Fig. 57). Pedipalps yellow

with few prolateral brownish stains. Labium and endites yellow with brownish margins. Sternum yellow with brown margins at base of legs, extending towards center along slight grooves. Legs yellow with brown longitudinal stains along ventral face of the femora and very slightly along tibiae. Abdomen cream colored with dark brown pattern of posterior median transversal stripes (Fig. 57). Total length 4.38. Carapace slightly domed, 2.38 long, 2.00 wide. Eye diameters: PME 0.16, ALE 0.16, PLE 0.16. Lateral eyes and chelicerae as in *S. championi.* Labium 0.26 long, 0.28 wide. Sternum 1.30 long, 1.00 wide. Leg measurements: I - femur 5.75/ patella 0.63/ tibia 5.63/ metatarsus 8.25/ tarsus 0.88/ total 21.14/ II – 4.13/ 0.63/ 3.75/ 5.13/ 0.75/ 14.39/ III – 2.50/ 0.63/ 2.25/ 3.00/ 0.63/ 9.01/ IV – 3.50/ 0.63/ 3.38/ 4.50/ 0.75/ 12.76. Ventral faces of femora I-II with double row of spines, prolateral row strong and twice as long as less developed retrolateral row (Fig. 10). Palpal femur with stridulatory pick as in *S. championi.* Cymbium with single distal spine (Fig. 58). Bulb 0.50 long. Distal area bifid (Figs. 58, 59). Abdomen 2.00 long, 1.63 wide, rounded, covered with slender hairs.

Female (paratype).—Coloration as in male. Total length 6.25. Carapace slightly domed, 3.50 long, 2.75 wide. Eye diameters: PME 0.16, ALE 0.14, PLE 0.14. Lateral eyes and chelicerae as in male. Labium 0.38 long, 0.32 wide. Sternum 1.80 long, 1.30 wide. Leg measurements: I - femur 4.00/ patella 0.75/ tibia 4.38/ metatarsus 5.75/ tarsus 0.88/ total 15.76/ II - 4.75/ 0.75/ 3.25/ 4.13/ 0.88/ 13.76/ III - 2.38/ 0.75/ 2.13/ 2.63/ 0.75/ 8.64/ IV - 3.50/ 0.63/ 3.25/ 3.63/ 0.88/ 11.89. Epigynal fovea conspicuous and deep. Positioning ridge semicircular (Fig. 60). Internal genitalia with pair of posterior seminal receptacles positioned close together with lateral sclerotized area (Fig. 61). Abdomen 2.75 long, 2.63 wide as in male.

Variation.—*Males:* total length 4.38–5.50; carapace 2.38–2.75; femur I 5.75–6.88; bulb 0.50–0.54 (*n* = 4). *Females:* Total length 6.25–6.75 (*n* = 3).

Distribution.—Costa Rica.

Material examined.-**COSTA RICA:** *Puntarenas Province, Monteverde Community* (1480 m), 1♂, July 1978, C.L. Craig & P. Class (MCZ); He-
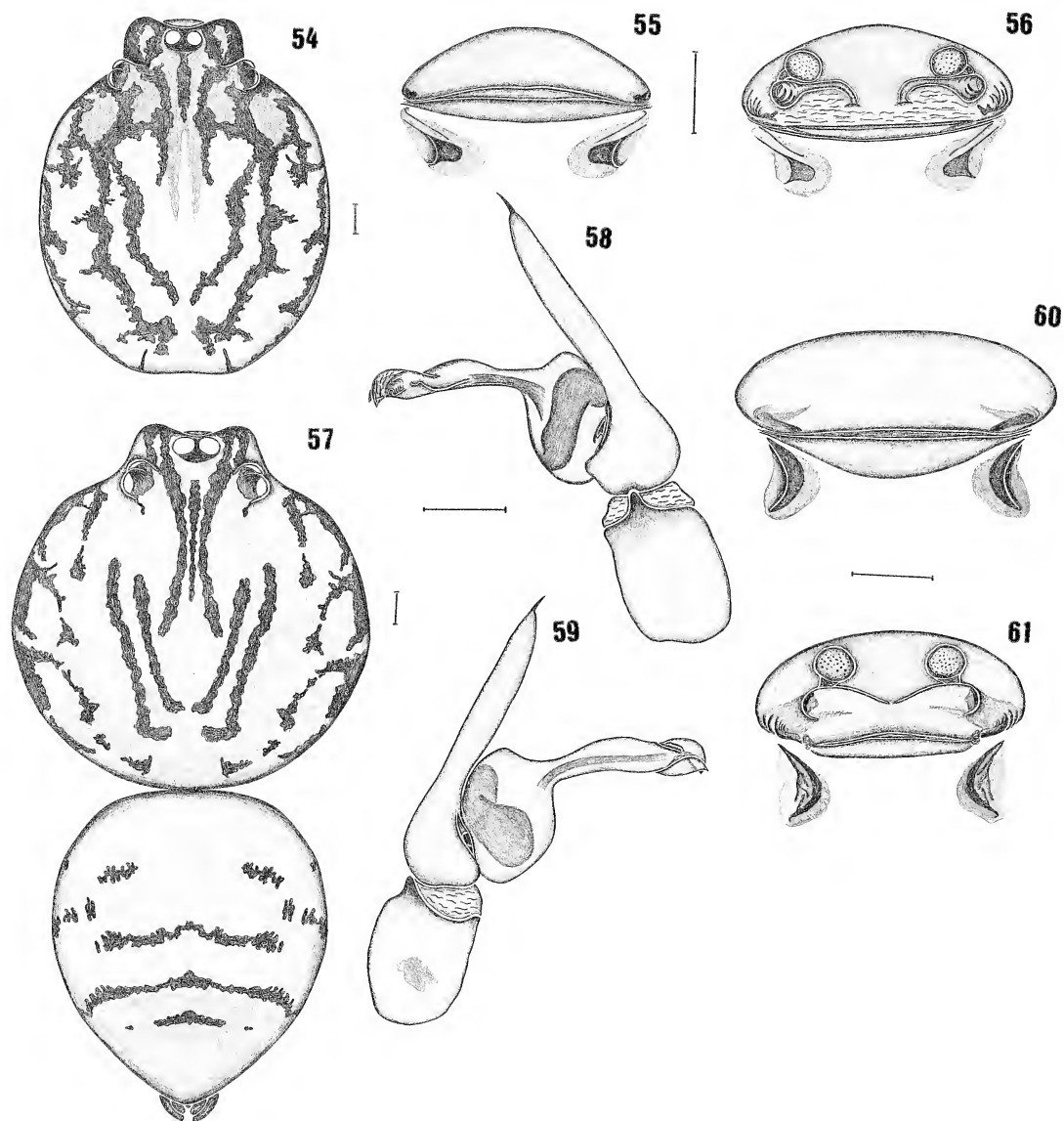
Figures 54–61.—54–56. *Scytodes zamorano* new species. 54. Female carapace, dorsal view; 55. Female epigynum, ventral view; 56. Dorsal view. 57–61. *Scytodes armata* new species. 57. Male body, dorsal view; 58. Male palp retrolateral view; 59. Prolateral view; 60. Female epigynum, ventral view; 61. Dorsal view. Scale lines = 0.25 mm.

redia, La Selva near Puerto Viejo, 1♂, 18 January 1979, J. Coddington (MCZ).

Scytodes gertschi Valerio
(Figs. 62–66)

Scytodes gertschi Valerio 1981: 86, figs. 6, 15, 27, 30 (male holotype and female allotype from Barro Colorado Island, Canal Zone, Panama, June 1950, A.M. Chickering deposited in MCZ, not examined) (examined by Valerio); Platnick 1989: 117.

Diagnosis.—The male of *S. gertschi* differs from the other species by the presence of a dorsal-ventrally elongated bulb (Fig. 64) and a dorsal triangular projection on the distal area of the male palpal bulb (Fig. 63). The female differs from the other species by the invaginated epigynal plate (Fig. 65) and subrectan-
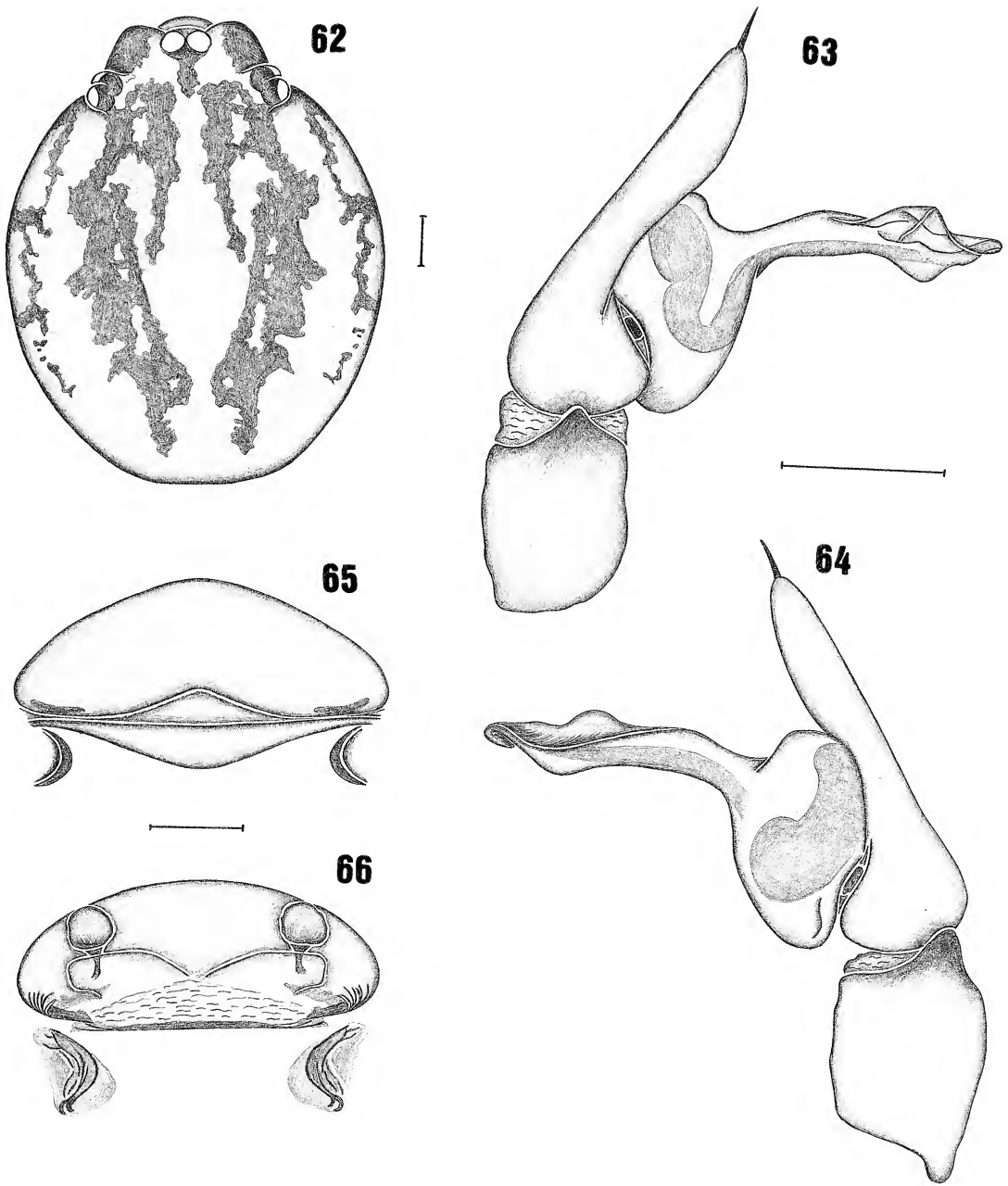
Figures 62–66.—*Scytodes gertschi* Valerio. 62. Male carapace, dorsal view; 63. Male palp, prolateral view; 64. Retrolateral view; 65. Female epigynum, ventral view; 66. Dorsal view. Scale lines = 0.25 mm.

gular pair of seminal receptacles (Fig. 66; Valerio 1981: fig. 15).

Variation.—*Males:* total length 3.00–3.75; carapace 1.63–1.88; bulb 0.36–0.40 (*n* = 2). *Females:* total length 3.63–4.50; carapace 1.75–2.00; femur I: 1.38–1.88 (*n* = 7).

Material examined.—PANAMA: *Canal Zone:*

Barro Colorado Island, 1♀, 11 February 1936, W.J. Gertsch (AMNH); Balboa, 2♂7♀ & 17 juvs., May 1964, A.M. Chickering (MCZ).

Scytodes cubensis Alayón
(Figs. 67, 68)

Scytodes cubensis Alayón 1977: 2, figs. 1a–c (female holotype from Loma Montecristi, Colorado,
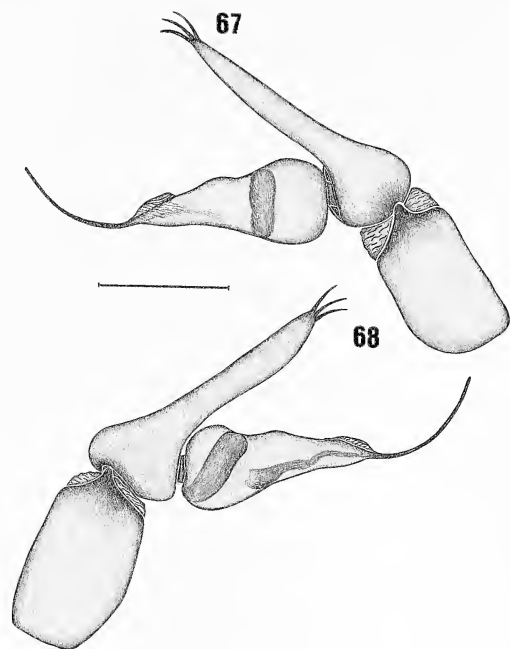
Figures 67–68.—*Scytodes cubensis* Alayón. 67. Male palp, retrolateral view; 68. Prolateral view. Scale lines = 0.25 mm.

Limonar, Matanzas, Cuba, March 1976, L.R. Hernández; and several male and female paratypes, deposited in Academia de Ciências de Cuba, not examined); Brignoli 1983: 149.

Male.—Described by Alayón 1977: 2, figs. 1a, b. Cymbium of palp with three slender distal spines (Fig. 67). Bulb long, distal area with a small dorsal membrane on base of long, filiform embolus (Figs. 67, 68).

New records.—TRINIDAD & TOBAGO: *Mount St. Benedict* (10°39′49″N, 61°23′56″W), 1♂2♀ (possible females, lacking abdomen), 27–30 June 1999, R.Pinto-da-Rocha (MZUSP 18860).

LITERATURE CITED

Alayón, G. 1977. Nuevas especies de *Scytodes* Latreille, 1804 (Araneae, Scytodidae) de Cuba. Poeyana 177:1–20.

Alayón, G. 1985. El género *Scytodes* Latreille, 1804 (Araneae: Scytodidae), en Jamaica, com la descripción de dos nuevas especies. Poeyana 293:1–10.

Alayón, G. 1992. Nueva especie de *Scytodes* y descripción del macho de *S. noeli* (Araneae: Scytodidae). Poeyana 413:1–7.

Banks, N. 1929. Spiders from Panama. Bulletin of the Museum of Comparative Zoology 69: 53–95.

Brescovit, A.D. & H. Höfer. 1999. Four new species of litter inhabiting *Scytodes* spiders (Araneae, Scytodidae) from Amazonas. Studies on Neotropical Fauna & Environment, 34:105–113.

Brescovit, A.D. & C.A. Rheims. 2000. On the synanthropic species of the genus *Scytodes* Latreille (Scytodidae, Araneae) of Brazil, with synonymies and records of these species in other Neotropical countries. Bulletin of the British Arachnological Society 11(8):320–330.

Brignoli, P.M. 1976. Beiträge zur Kenntnis der Scytodidae (Araneae). Revue Suisse de Zoologie 83(1):125–191.

Brignoli, P.M. 1983. A Catalogue of The Araneae Described Between 1940 and 1981. Manchester, Manchester Acad., 755 p.

Caporiacco, L. di. 1947. Diagnosi preliminari di specie nuove di Aracnidi della Guiana Britannica, reccolte dai professori Beccari e Romiti. Monitore Zoologico Italiano 56:20–34.

Caporiacco, L. di. 1948. Arachnida of British Guiana collected in 1931 and 1936 by Professors Beccari and Romiti. Proceedings of Zoology of the Society of London 118(3):607–747.

Höfer, H. 1990. The spider community (Araneae) of a central Amazonian blackwater inundation forest (igapó). Acta Zoologica Fennica 190:173–179.

Nentwig, W. 1993. Spiders of Panama. Flora & Fauna Handbook nº12, The Sandhill Crane Press, Inc., 274 p.

Pickard-Cambridge, F.O. 1899. Arachnida - Araneida. Pp. 48–52. *In* Biologia Centrali-Americana. Godman & Salvin, London, vol. 2.

Platnick, N.I. 1989. Advances in Spider Taxonomy 1981–1987. Manchester Univ. Press, Manchester, 673 p.

Rheims, C.A. & A.D. Brescovit. 2000. Six new species of *Scytodes* Latreille 1804 (Araneae, Scytodidae) from Brazil. Zoosystema 22(4):721–731.

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Bruxelas, vol. 1, Pp. 1–1040.

Simon, E. 1892. Voyage de M. Simon en Vene-
zuela, Arachnida. Annales de la Société. Ento-
mologique de France 61:423–462.

Valerio, C.E. 1981. Spitting spiders (Araneae, Scy-
todidae, *Scytodes*) from Central America. Bulle-
tin of the American Museum of Natural History
170:80–89.

A REVIEW OF THE CHINESE PSECHRIDAE (ARANEAE)

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ABSTRACT. The Chinese psechrid spiders of the genera *Fecenia* and *Psechrus* are reviewed. The species *Fecenia hainanensis* is newly synonymized with *F. cylindrata*. The species *P. mimus* is considered a nomen dubium. The species *P. senoculata* is regarded as a valid species. The male is newly described for *P. tingpingensis*. Three new species are described: *P. jinggangensis* new species, *P. rani* new species, and *P. taiwanensis* new species. In all, nine psechrid species are recognized from China. The spinnerets, trichobothria, and tarsal organ morphology of *P. tingpingensis* are presented. A key to Chinese *Psechrus* species is also provided.

Keywords: Psechridae, *Psechrus*, *Fecenia*, China

Psechrid species of the genera *Fecenia* Simon 1887 and *Psechrus* Thorell 1878 are widespread from China (north to Qinling Mt., Shaanxi) and southeast Asia to New Guinea, with approximately 19 valid species (Platnick 2000). A revision of this family was presented by Levi (1982), who gave detailed diagnoses, illustrations, and descriptions of the family, genera, and species. Levi's revision (1982) enabled further work on the species of this family possible (e.g., Murphy 1986; Yin, Wang & Zhang 1985). To date, seven psechrid species have been reported from China (Song, Zhu & Chen 1999): *P. ghecuanus* Thorell 1897; *P. kunmingensis* Yin, Wang & Zhang 1985; *P. minus* Chamberlin 1924; *P. sinensis* Berland & Berland 1914; *P. tingpingensis* Yin, Wang & Zhang 1985; *Fecenia cylindrata* Thorell 1895; and *F. hainanensis* Wang 1990. The presence of *P. torvus* (O. P.-Cambridge 1869) in Taiwan (Lee 1966; Hu 1984) was shown to be a misidentification (Chen 1996; Song, Zhu & Chen 1999).

Further collection and study of Chinese psechrids made this revision possible. In this paper, nine psechrid species are recognized from China. The species *Fecenia hainanensis* is newly synonymized with *F. cylindrata*. The species *P. mimus*, which was described

based on an unidentifiable juvenile female (Chamberlin 1924), is considered a nomen dubium, and therefore the species *P. senoculata* is removed from its synonymy. The male is newly described for *P. tingpingensis*. The female previously identified as *P. sinensis* by Levi (1982) is shown to be a new species. Three new species described in this study are: *P. jinggangensis*; *P. rani*; and *P. taiwanensis*.

METHODS

All measurements are in mm. All scales are 0.2 mm length. Leg measurements are shown as: total length (femur, patella + tibia, metatarsus, tarsus). The terms used in the genitalic descriptions follow Levi (1982). Because of the similar body color pattern, stable number of cheliceral teeth, and similar leg spine distributional pattern at species-level, the species descriptions are focused on the male and female genitalic structures. The material used in this study was based on collections made available through the courtesy of the following individuals and institutions: N.I. Platnick, American Museum of Natural History, New York, USA (AMNH); J. Margerison, The Natural History Museum, London, UK (BMNH); C.M. Yin, Hunan Biological Institute, Changsha, Hunan, China (HBI);

M.S. Zhu, Hebei Teachers University, Shijiazhuang, China (HTU); J. Chen, Institute of Zoology, Beijing, China (IZB); P. Pantini, Museo de Bergamo, Bergamo, Italy (MCB); C. Rollard, Museum National d'Histoire Naturelle, Paris, France (MNHN).

SPINNERETS, TRICHOBOTHRIA AND TARSAL ORGAN MORPHOLOGY

A representative species, *Psechrus tingpingensis*, was chosen here for detailed spinnerets, trichobothria, and tarsal organ descriptions in order to form a basis for further comparison with other psechrids and also with other families in future study. This species was selected for the reason of well-preserved spinnerets in the examined psechrid species and large numbers of available specimens.

Cribellum large, divided, female with numerous spigots (Figs. 39, 40), male without spigots (Fig. 41). According to a study by Zhang et al. (1998) of the female juvenile cribellum of *P. mimus* (sensu Zhang et al. 1998), "there was still not any spigot visible on the seventh day of molting; there were few small spigots in the middle area of cribellum on the ninth day of molting, and many spigots appeared on the eleventh day juveniles but still no distinct segment." Apex of anterior lateral spinneret (ALS) with two major ampullate spigots (MAP) at mesal margins, many short piriform spigots in both male and female; posterior median spinneret (PMS) strongly curved back anteriorly (Fig. 36), with spigots situated on distal half of the segment, one minor ampullate spigots (mAP) on distal end, 40–50 aciniform spigots in both male and female, and 11–12 cylindrical spigots (as shown in short arrows) in female arranged in two rows; posterior lateral spinneret (PLS) with approximately 30 aciniform spigots in both male and female, and at least 16 cylindrical spigots (as shown in short arrows) in female (Figs. 42–47). Trichobothrial base with hood transversely striated (Fig. 37). Tarsal organ oval to round (Fig. 38), situated dorsally on distal tarsus, slightly anterior of most distal trichobothrium.

KEYS TO CHINESE *PSECHRUS* SPECIES

Males

1. Palpal femur modified with notch (Figs. 21, 26, 33) 2
   Palpal femur without such modification 4
2. Conductor base enlarged, with small tubercles (Fig. 19) . . . . *senoculata*
   Conductor base not enlarged, without tubercles 3
3. Embolic base with 2 teeth (Figs. 31, 32) . . . . *tingpingensis*
   Embolic base with only 1 tooth (Figs. 24, 25) . . . . *sinensis*
4. Embolus short, much shorter than the bulb length (Figs. 5, 6) . . . . *ghecuanus*
   Embolus long, at least the bulb length (Figs. 13, 14) . . . . **rani** new species

Females

1. Ventral abdomen with distinct white spot in front of cribellum 2
   Ventral abdomen without distinct white spot in front of cribellum 7
2. Epigynum with slits more or less parallel (Fig. 29) . . . . **taiwanensis** new species
   Epigynum otherwise (Figs. 9, 11, 22, 27, 34) 3
3. Epigynal median sclerite lobed on sides, spermathecal heads situated laterad of spermathecae (Figs. 9, 10) . . . . *kunmingensis*
   Epigynal median sclerite not lobed, spermathecal heads situated mesad of spermathecae (Figs. 11, 12, 22, 23, 27, 28, 34, 35) 4
4. Slits of epigynum wider apart anteriorly than posteriorly (Figs. 11, 22) 5
   Slits of epigynum wider apart posteriorly than anteriorly (Figs. 27, 34) 6
5. Posterior copulatory ducts much larger than spermathecae (Fig. 23) . . . . *senoculata*
   Posterior copulatory ducts much smaller than spermathecae (Fig. 12) . . . . **jinggangensis** new species
6. Anterior epigynum strongly narrowed, width approximately ¼ of posterior (Fig. 27) . . . . . . *sinensis*
   Anterior epigynum moderately narrowed, width at least ½ of posterior (Fig. 34) . . . . . *tingpingensis*
7. Spermathecal heads situated mesad of spermathecae (Fig. 16) . . . . **rani** new species
   Spermathecal heads situated anterad of spermathecae (Fig. 8) . . . . *ghecuanus*
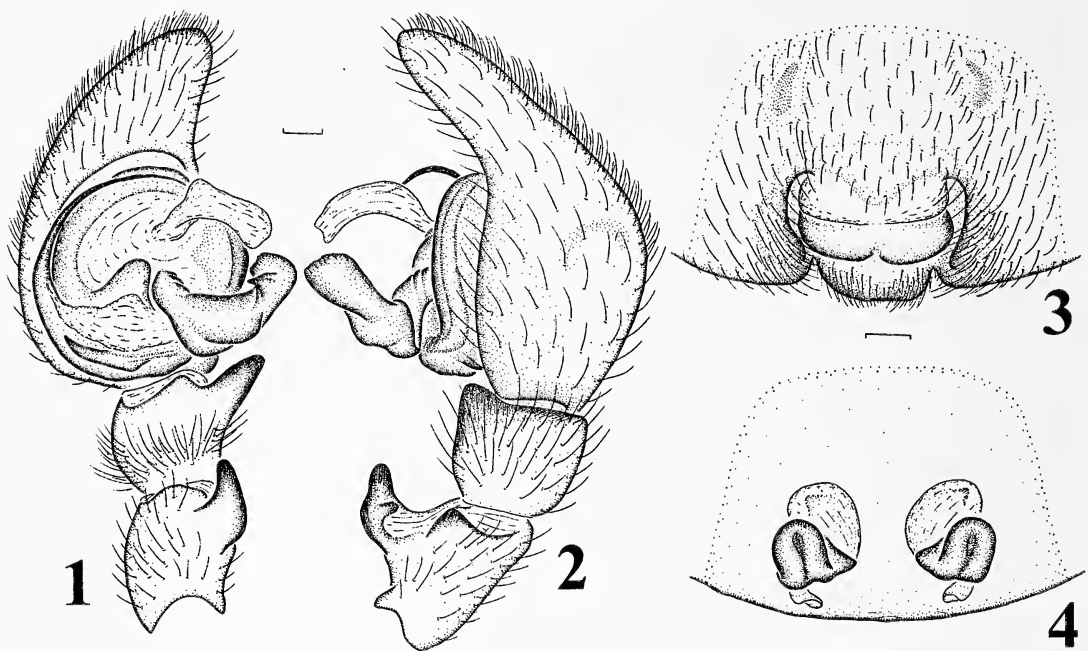
Figures 1–4.—*Fecenia cylindrata*. 1. Male palp, ventral view; 2. Male palp, retrolateral view; 3. Epigynum; 4. Vulva.

TAXONOMY

Fecenia cylindrata Thorell
Figs. 1–4, Map 1

Fecenia cylindrata Thorell 1895: 64 (1 juv. syntype from Tharrawaddy, Myanmar, in Naturhistoriska Riksmuseet, Stockholm, examined by Levi

1982). Thorell 1897: 263; Pocock 1900: 212; Lehtinen 1967: 462, figs. 472, 473 (male); Levi 1982: 136, figs. 80–82 (male and female); Yang & Wang 1993: 29, figs. 1–4 (male and female); Song, Zhu & Chen 1999: 397, fig. 231O-Q (male and female).

Fecenia hainanensis Wang 1990: 257, figs. 1–3 (female holotype from Tongqian City, Hainan, China, in HBI, examined). Song, Zhu & Chen 1999: 397. NEW SYNONYMY.

Synonymy.—This species was erroneously described as *F. hainanensis* with one female specimen from Hainan, China. The only difference between *F. hainanensis* and *F. cylindrata*, according to Wang (1990), was the presence of a pair of long, oval, white spots on ventral abdomen. Apparently, such spots are present in *F. cylindrata* and other *Fecenia* species (Levi 1982). Later collection of *F. cylindrata* with both males and females from the same locality (Yang & Wang 1993) further showed that *F. hainanensis* is in fact a junior synonym of *F. cylindrata*. The species *F. cylindrata* was collected from Tongqian and Qionghai, Hainan, China (Wang 1990; Yang & Wang 1993). It is widespread and occurs in large numbers in Qionghai (Yang & Wang 1993).
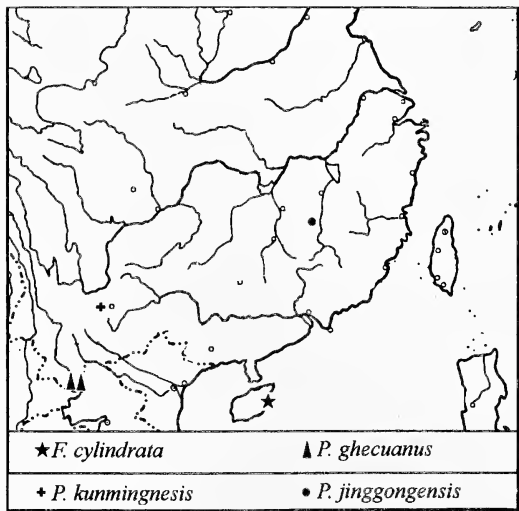
Map 1.—Distribution of *Fecenia cylindrata*, *Psechrus ghecuanus*, *P. kunmingensis* and *P. jinggangensis* new species in China.
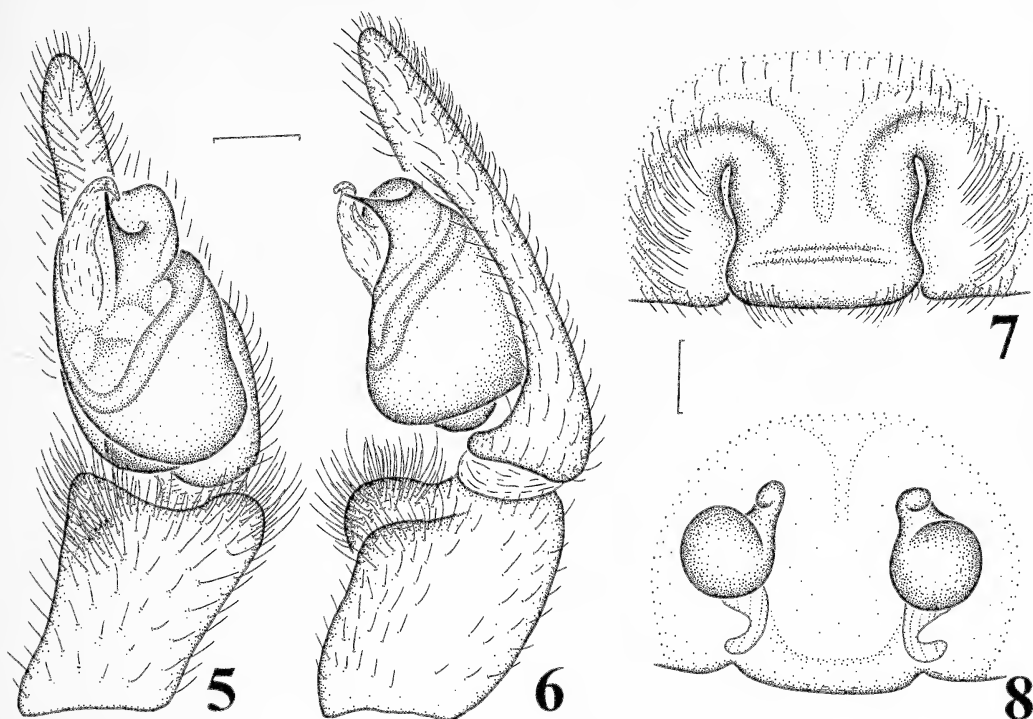
Figures 5–8.—*Psechrus ghecuanus*. 5. Male palp, ventral view; 2. Male palp, retrolateral view; 3. Epigynum; 4. Vulva.

Diagnosis.—This species can be distinguished from others by the presence of a median depression on the epigynum, and by the shape and transverse direction of the median apophysis (Figs. 1–4).

Description.—See Thorell (1895), Levi (1982) and Wang (1990).

Material examined.—CHINA: *Hainan:* Jianfeng, 6 August 1990, 1 male and 1 female (M.B. Gu, HTU); Tongqian, 1 July 1984, female holotype of *F. hainanensis* Wang 1990 (M.Y. Liu, HBI).

Distribution.—China (Hainan) (Map 1), Myanmar.

Psechrus ghecuanus Thorell
Figs. 5–8; Map 1

Psechrus ghecuanus Thorell 1897: 261 (female syntypes from Myanmar, in Naturhistoriska Riksmuseet, Stockholm, examined by Levi 1982); Levi 1982: 123, figs. 29–33 (female); Yin, Wang & Zhang 1985:19, fig. 1 (A-I)(male and female); Song, Zhu & Chen 1999: 397, figs. 232A-B, M-N (male and female).

Diagnosis.—This species is similar to *P. torvus* but can be distinguished by the short embolus, the simple embolic base (Figs. 5, 6), and the more or less parallel epigynal slits (Figs. 7, 8).

Male.—See description of Yin, Wang & Zhang (1985). White spot in front of cribellum absent. Male palpal femur without modification; palpal bulb duct more or less strongly curved, U-shaped; conductor long, lamella shaped; embolus short, slender; embolic base simple, not rectangular, but slightly triangular (Figs. 5, 6).

Female.—See descriptions of Thorell (1897), Levi (1982), and Yin, Wang & Zhang (1985). White spot in front of cribellum absent. Epigynal slits more or less parallel; epigynal median sclerite wide, width about 1.25× length; copulatory ducts short, not distinct; spermathecal heads apparent, situated anteriorly; spermathecae rounded, large, widely separated (Figs. 7, 8).

Material examined.—CHINA: *Yunnan:* Mengla, 21 March 1978, 1 male and 1 female (J.F. Wang, HBI); Menglun, 31 July 1981, 2 females (J.F. Wang, HBI); Menghai, 23 March 1978, 1 male and 1 female (J.F. Wang, HBI).
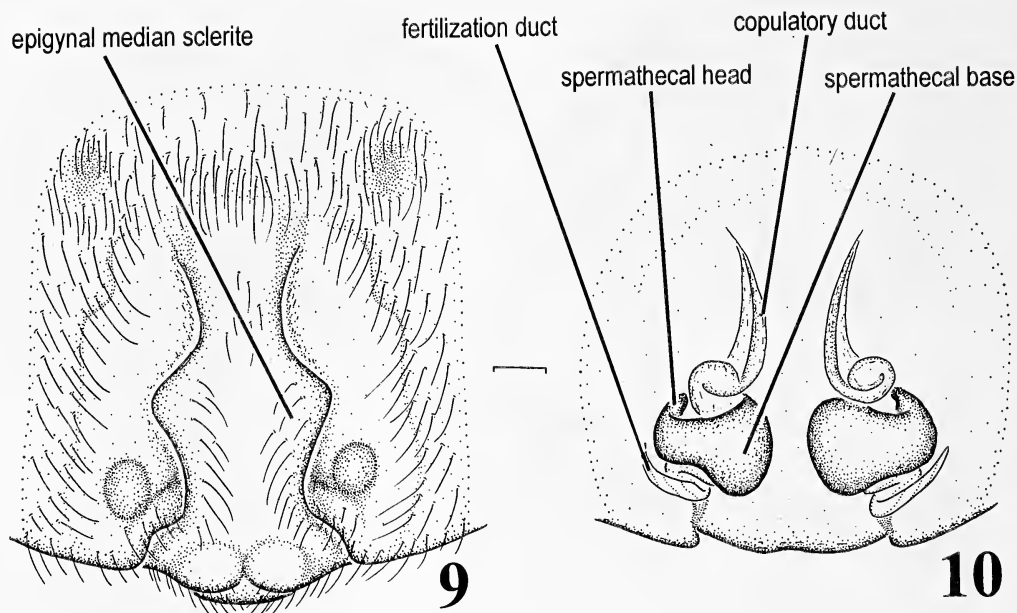
Figures 9, 10.—*Psechrus kunmingensis*, female. 9. Epigynum; 10. Vulva.

Distribution.—China (Yunnan) (Map 1), India, Thailand, Myanmar.

Psechrus kunmingensis Yin, Wang & Zhang
Figs. 9, 10; Map 1

Psechrus kunmingensis Yin, Wang & Zhang 1985: 25, fig. 5(A-D) (female holotype and 3 female paratypes from Kunming, Yunnan, China, in HBI, examined). Song, Zhu & Chen 1999: 397, figs. 232C-D, O-P (male and female).
Psechrus tingpingensis: Feng 1990: 34, fig. 9 (female only) (misidentification).

Diagnosis.—This species can be easily distinguished by the laterally lobed epigynal median sclerite, the lateral placement of the spermathecal heads, the shape of spermathecae (Figs. 9, 10) and the presence of strong apophyses at embolic base.

Female.—Described by Yin, Wang & Zhang (1985). White spot in front of cribellum present. Epigynal slits not parallel; epigynal median sclerite elongated, with lateral margins lobed; copulatory ducts long, distinct, widely separated; spermathecal heads apparent, situated laterally, curved anteriorly; spermathecae transversely extended, large, widely separated (Figs. 9, 10).

Male.—Illustrated by Song, Zhu & Chen (1999), but not described. The male specimens are not available in this study. Judging from the illustrations by Song, Zhu & Chen

(1999), male palpal bulb duct only slightly U-shaped; conductor long, lamella shaped; embolus short, slender; embolic base with strong apophyses (figs. 232O-P in Song, Zhu & Chen 1999).

Material examined.—CHINA: *Yunnan:* Kunming, 5 April 1979, female holotype (J.F. Wang, HBI); Kunming, July 1983, 2 female paratypes (M.Y. Liu, HBI); Kunming, 21 July 1981, 4 females (J.F. Wang, HBI); Kunming, 30 June 1999, 1 female (X. Xu, HBI).
Distribution.—China (Yunnan) (Map 1).

***Psechrus jinggangensis* new species**
Figs. 11, 12; Map 1

Types.—Female holotype from Jinggang-shan (N26.5E114.1), Jiangxi, China (4 October 1996; C.M. Yin), deposited in HBI.
Etymology.—The specific name refers to the type locality.
Diagnosis.—This species is similar to *P. kunmingensis* but can be distinguished by the laterally concaved epigynal median sclerite, the rounded spermathecae, and the mesal placement of the spermathecal heads (Figs. 11, 12).
Female.—Total length 24.5. Carapace 9.0 long, 7.8 wide. Abdomen 15.5 long, 9.0 wide. Leg measurements: I: 63.2 (18.5, 22.2, 15.1, 7.4); II: 47.3 (13.0, 16.5, 12.0, 5.8); III: 33.5 (10.0, 10.5, 8.5, 4.5); IV: 46.0 (14.0, 15.5,
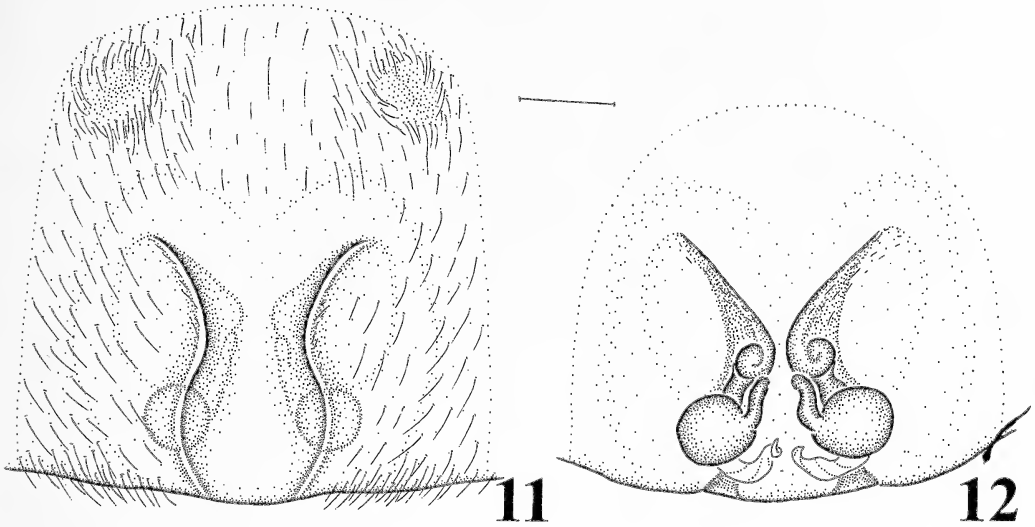
Figures 11, 12.—*Psechrus jinggangensis*, female. 11. Epigynum; 12. Vulva.

11.0, 5.5). White spot in front of cribellum present. Epigynal slits not parallel; epigynal median sclerite elongated, with lateral margins concave; copulatory ducts widely separated anteriorly, approaching each other posteriorly; spermathecal heads apparent, situated mesally; spermathecae rounded, widely separated (Figs. 11, 12).

Male.—Unknown.

Other material examined.—None.

Distribution.—China (Jiangxi) (Map 1).

Psechrus rani new species
Figs. 13–18; Map 2

Types.—Male holotype from Sanchahe, Maolan National Nature Reserve, Libo, Guizhou, China (6 October 1997; X.P. Wang); female paratype from Xiaoqikong, Libo, Guizhou, China (2 March 1995; J.C. Ran), deposited in IZB.

Etymology.—The specific name is a patronym in honor of Mr. Jing-Cheng Ran of the research department, Maolan National Natural Reserve, Guizhou, China, the collector of the paratype female.

Notes.—The male and female are matched because their localities are close together and also the similar size.

Diagnosis.—This new species seems closest to *P. torvus* but can be distinguished by the simple, small embolic base, the enlarged conductor base (Figs. 13, 14), and the more or less parallel lateral margins of epigynal me-

dian sclerite, and the shape of spermathecae (Figs. 15, 16).

Male.—Total length 18.0. Carapace 7.2 long, 5.6 wide. Abdomen 10.8 long, 4.8 wide. Leg measurements: I: 69.6 (18.4, 23.2, 19.2, 8.8); II: 53.4 (14.4, 18.0, 14.0, 7.0); III: 33.6 (9.6, 11.2, 9.2, 3.6); IV: 54.8 (15.2, 17.0, 15.0, 7.6). White spot in front of cribellum absent. Male palpal femur without modification; palpal bulb duct simply curved, slightly U-shaped; conductor long, lamella shaped, with enlarged base; embolus long, slender; embolic base simple, small, not rectangular (Figs. 13, 14).

Female.—Total length 21.6. Carapace 8.0 long, 6.0 wide. Abdomen 13.6 long, 8.0 wide. Leg measurements: I: 54.8 (14.8, 18.4, 14.4, 7.2); II: 44.2 (12.4, 15.2, 11.0, 5.6); III: 31.2 (9.2, 9.6, 8.0, 4.4); IV: 46.2 (12.8, 14.4, 12.0, 7.0). White spot in front of cribellum absent. Epigynal slits more or less parallel; epigynal median sclerite with lateral margins wide apart medially, posteriorly, approaching each other anteriorly; width of epigynal median sclerite approximately 1.5× length; copulatory ducts short but clearly visible; spermathecal heads apparent, short, situated mesally; spermathecae rounded, widely separated (Figs. 15, 16).

Penultimate instar.—As indicated by Levi (1982), some sclerotized sculpturing occurs in the genital area in the penultimate instar. In
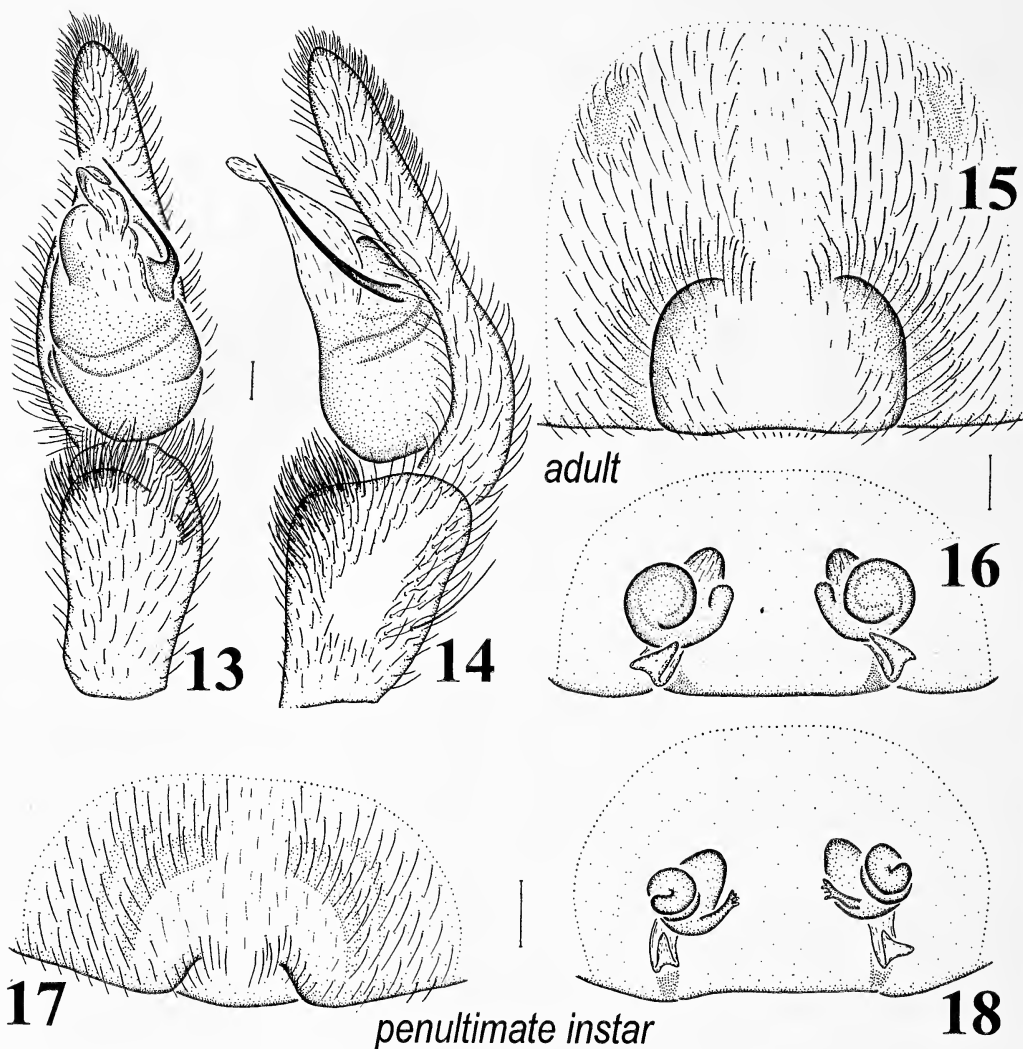
Figures 13–18.—*Psechrus rani* new species. 13. Male palp, ventral view; 14. Male palp, retrolateral view; 15. Epigynum; 16. Vulva; 17. Penultimate instar, epigynum; 18. Penultimate instar, vulva.

the penultimate instar, the epigynum and vulva (Figs. 17, 18) are clearly apparent and may be confused with adults stage (Figs. 15, 16), if no adults are collected and compared with it. Compared to the adult stage, the longitudinal grooves of the epigynum of the penultimate instar are much shorter and not well developed, and the spermathecae and spermathecal heads are weaker, although the copulatory ducts and fertilization ducts are as well developed as the adult stage. Perhaps this is one reason why the psechrid female genitalia appear so variable. According to our collection of *P. senoculata* from various places in China, including Shaanxi, Hubei, Sichuan, Hubei, Hunan, and Guizhou Province, all adult female genitalia are stable, particularly the vulva.

Other material examined.—**CHINA:** *Guizhou:* Libo, Maolan National Nature Reserve, Yaozai, 7 October 1997, 1 female penultimate instar (X.P. Wang, IZB).

Distribution.—China (Guizhou) (Map 2).

Psechrus senoculata Yin, Wang & Zhang
Figs. 19–23; Map. 2

Psechrus mimus: Xu & Wang 1983: 35, figs. 1–7 (male and female); Song 1987: 68, figs. 34A-D (male and female); Song 1988: 33; Chen & Zhang 1991: 40, fig. 31 (male and female); Zhang
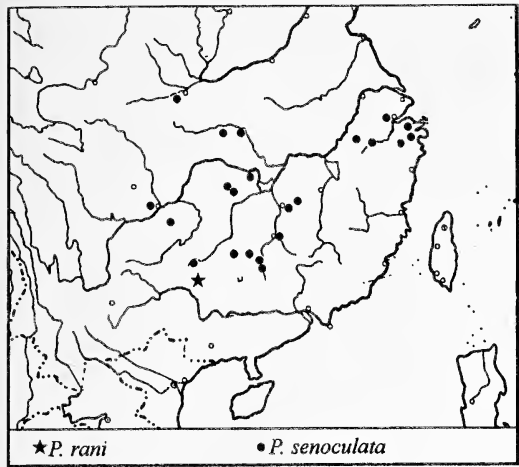
Map 2.—Distribution of **Psechrus rani** new species and *P. senoculata* in China.

et al. 1998: 77, figs. 2a-p (female); Song, Zhu & Chen 1999: 397, figs. 232E-F, Q-R, Pl. 3C (female) (misidentification).

Psechrus sinensis: Hu 1984: 55, fig. 50 (male and female); Chen & Gao 1990: 25, figs. 27a-b (male and female) (misidentification).

Psechrus senoculata Yin, Wang & Zhang 1985: 21. fig. 2(A-J) (female holotype from Sangzhi, Hunan, male allotype from Zhangjiajian, Daiyong, Hunan, and 1 male and 1 female paratypes from Huanglongdong, Hangzhou, Zhejiang, China, in HBI, examined. Feng 1990: 33, fig. 8 (male and female).

Synonymy.—The species *P. senoculata* has been treated as a junior synonym of either *P. mimus* (Song 1988) or identified as *P. sinensis* (see Hu 1984; Chen & Gao 1990). Chamberlin (1924) described *P. mimus* from an unidentifiable female juvenile from Su-
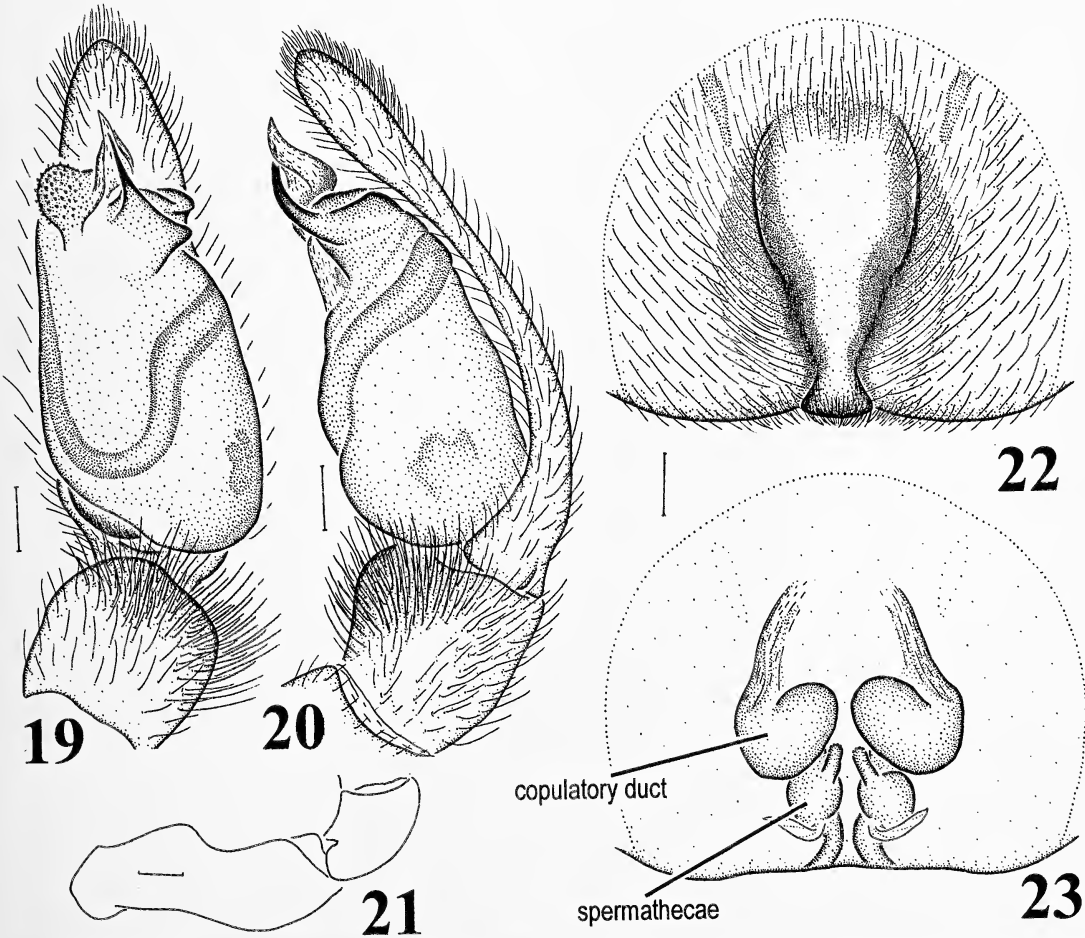
Figures 19–23.—*Psechrus senoculata*. 19. Male palp, ventral view; 20. Male palp, retrolateral view; 21. Male palpal femur, showing femoral modification; 22. Epigynum; 23. Vulva.
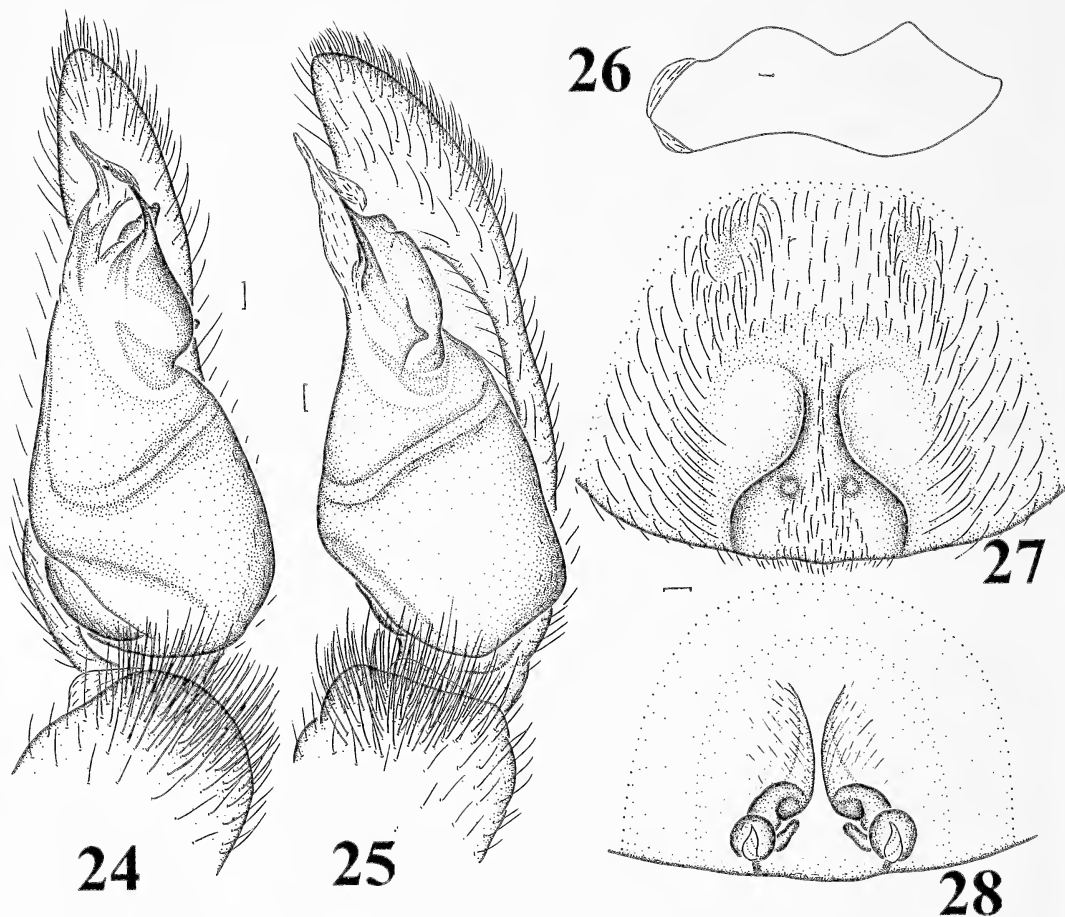
Figures 24–28.—*Psechrus sinensis*. 24. Male palp, ventral view; 25. Male palp, retrolateral view; 26. Male palpal femur, showing femoral modification; 27. Epigynum; 28. Vulva.

zhou, Jiangsu, China and should be considered as nomen dubium. Further study of the types of *P. sinensis (two male syntypes from Guiyang, Guizhou, China, in MNHN, examined) showed that P. senoculata* is a valid species rather than the synonym of *P. sinensis*.

Diagnosis.—This species can be easily distinguished from *P. sinensis* by the elongated, vase-shaped, anteriorly wider epigynal median sclerite (Fig. 22), the large, strongly expanded posterior part of copulatory ducts (Fig. 23), and the strongly enlarged, tuberculous conductor base (Fig. 19).

Male.—Described by Yin, Wang & Zhang (1985) and Song (1987). White spot in front of cribellum present. Palpal femur modified with notch (Fig. 21); palpal bulb duct U-shaped; conductor short, lamella shaped; conductor base strongly enlarged, with numerous

small tubercles; embolus short, slender, with rectangular base (Figs. 19–21).

Female.—Described by Yin, Wang & Zhang (1985) and Song (1987). White spot in front of cribellum present. Epigynal slits wider apart anteriorly than posteriorly; epigynal median sclerite vase-shaped; copulatory ducts with posterior part enlarged, extending anteriorly; spermathecal heads apparent; spermathecae rounded, relatively small, close to each other (Figs. 22, 23).

Material examined.—CHINA: *Hunan:* Sangzhi, 21 August 1984, female holotype (Y.J. Zhang, HBI); Daiyong, Zhangjiajian, 20 September 1984, male allotype (Y.J. Zhang, HBI); Chengbu, July 1982, 2 females (X.C. Ouyang, HBI); Liuyang, Mt. Dawei, 31 July 1994, 1 female (H.M. Yan, HBI); Changsha, Lukou, 30 June 1999, 1 female (Xu, HBI); Daoxian, 9 October 1991, 1 male (L.S. Gong,
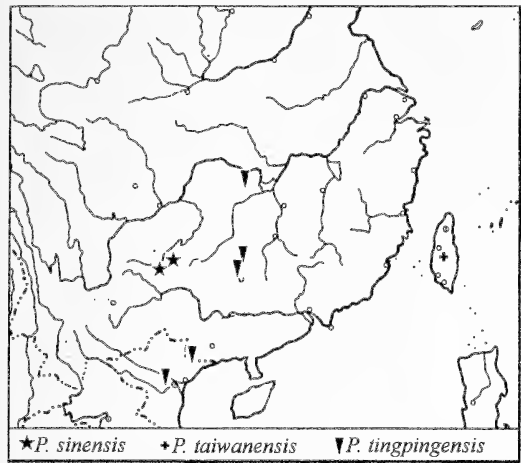
Map 3.—Distribution of *Psechrus sinensis*, *P. taiwanensis* new species, and *P. tingpingensis* in China and Vietnam.

HBI); Shimen, Mt. Huping, 25 June–7 July 1992, 1 female (X.J. Peng, HBI); Suining, 25 May 1995, 2 females (C.M. Yin & Y.J. Zhang, HBI); Hengyang, Mt. Goulou (elev. 1500 m), 30 July 1997, 1 female (X.J. Peng, HBI); Shuangpai, 11 August 1993, 1 female (C.M. Yin, HBI). *Hubei:* Wudangshan, from Zixiao to Nanya, 23 September 1997, 1 male and 4 females (X.P. Wang, AMNH); Xiangyang, October 1990, 1 male and 3 females (J.F. Wang, HBI). *Guizhou:* Kaili, 3 October 1997, 1 male and 1 female (X.P. Wang, MCB); Zunyi, 22 September 1997, 1 female (X.P. Wang, AMNH). *Sichuan:* Chunqing, Jingyunshan, 26 September 1997, 1 female (X.P. Wang, AMNH). *Zhejiang:* Hangzhou, Huanglongdong, 16 May 1982, 1 male and 1 female paratypes (Z.F. Chen, HBI). *Shaanxi:* Zhouzhi, Louguantai, June 1990, 1 male and 1 female (X.P. Wang, AMNH).

Distribution.—China (Hunan, Zhejiang, Hubei, Guizhou, Sichuan, Shaanxi) (Map 2).

Psechrus sinensis Berland & Berland 1914
Figs. 24–28, Map 3

Psechrus sinensis Berland & Berland 1914: 131, figs. 1–3 (two male syntypes from Guiyang, Guizhou, China, in MNHN, examined). Lehtinen 1967: 261, fig. 474 (male) (incorrectly synonymized with *P. singaporensis*); Levi 1982: 123, figs. 34, 35 (male only, female is *P. taiwanensis* sp. nov.); Song, Zhu & Chen 1999: 397, figs. 232G-H, S (male and female).

Psechrus guiyangensis Yin, Wang, & Zhang, 1985: 24, fig. 4(A-D) (female holotype and paratypes from Guiyang, Guizhou, China, in HBI, examined). First synonymized by Song, Zhu & Chen (1999).

Synonymy.—Study of *P. sinensis* male types and further collections of psechrids in China shows that *P. guiyangensis* is a junior synonym of *P. sinensis* (Song, Zhu & Chen 1999). As suspected by Levi (1982), the female (from Taiwan) illustrated as *P. sinensis* in Levi's (1982) paper is a new species *P. taiwanensis*, which will be described in this paper. Although Lehtinen (1967) listed *P. sinensis* as a junior synonym of *P. singaporensis*, this was not followed by later authors (Levi 1982; Platnick 1997; Platnick 2000). The species *P. sinensis* can be easily distinguished from *P. singaporensis* by the presence of white spot in front of cribellum, the strongly narrowed anterior part of epigynal median sclerite, the spermathecal shape, and the shape of conductor and embolic base.

Diagnosis.—This species is similar to *P. senoculata* but can be recognized by the ab-
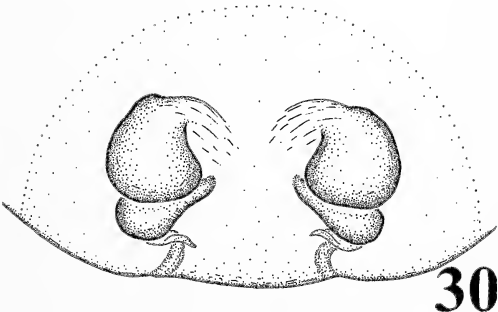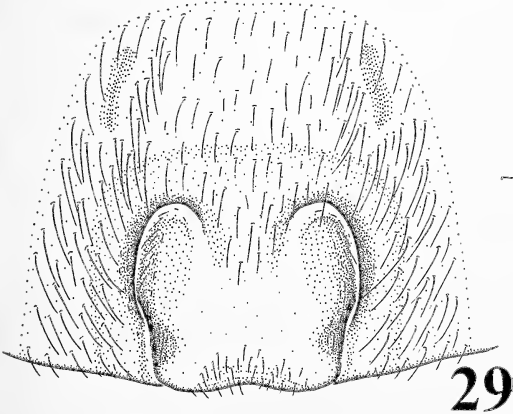
Figures 29, 30.—*Psechrus taiwanensis* new species, female. 29. Epigynum; 30. Vulva.
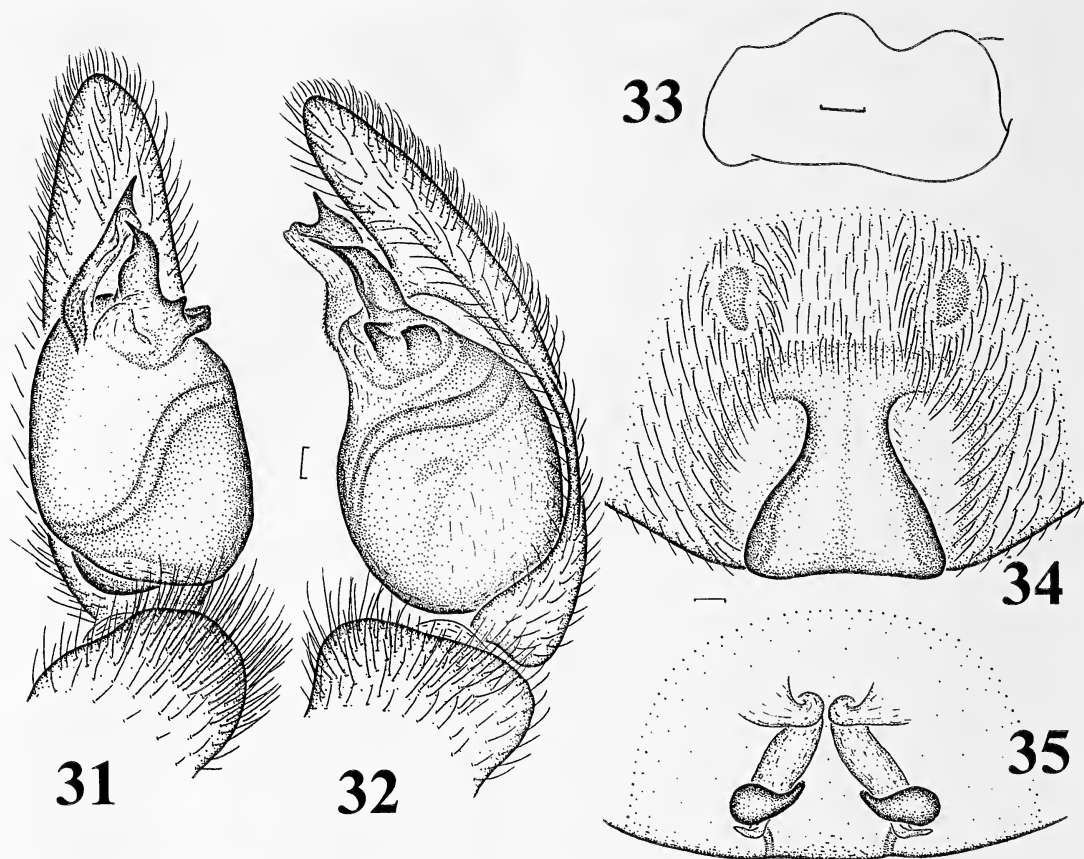
Figures 31–35.—*Psechrus tingpingensis*. 31. Male palp, ventral view; 32. Male palp, retrolateral view; 33. Male palpal femur, showing femoral modification; 34. Epigynum; 35. Vulva.

sence of tubercles on the conductor base, the different shape of the rectangular embolic base (Figs. 24, 25), and the anteriorly narrowed median epigynal sclerite, and the narrowly separated copulatory ducts (Figs. 27, 28).

Male.—Described by Berland & Berland (1914) and Levi's (1982). White spot in front of cribellum present. Palpal femur modified with notch (Fig. 26); palpal bulb duct simply curved, slightly U-shaped; conductor short, lamella shaped; conductor base normal, not enlarged; embolus short, slender; embolus with toothed rectangular base (Figs. 24–26).

Female.—See Yin, Wang & Zhang's (1985) description of *P. guiyangensis*. White spot in front of cribellum present. Epigynal slits approach each other anteriorly; epigynal median sclerite wider posteriorly than anteriorly, with anterior part only about ¼ width of posterior part; copulatory ducts narrowly separated medially, with anterior and posterior

part moderately separated; spermathecal heads apparent, situated mesally on spermathecae; spermathecae rounded, widely separated (Figs. 27, 28).

Material examined.—CHINA: *Guizhou:* Guiyang (Kouy-Tcheou, Env. De Kouy-Yang), 1909 and 1913, 2 male syntypes (Le P. Cavalerie, MNHN); Guiyang, 30 September 1997, 1 female (X.P. Wang, AMNH); Guiyang, 4 July 1983, female holotype and 4 female paratypes of *P. guiyangensis* (Y.J. Zhang, HBI); Anshun, 2 July 1999, 2 females (X. Xu, HBI).

Distribution.—China (Guizhou) (Map 3).

Psechrus taiwanensis new species
Figs. 29, 30, Map 3

Type.—Female holotype from Taiwan (1894; Holst), deposited in BMNH, examined.

Etymology.—The specific name refers to the type locality.

Diagnosis.—This species is similar to *P. rani* new species, but can be distinguished by
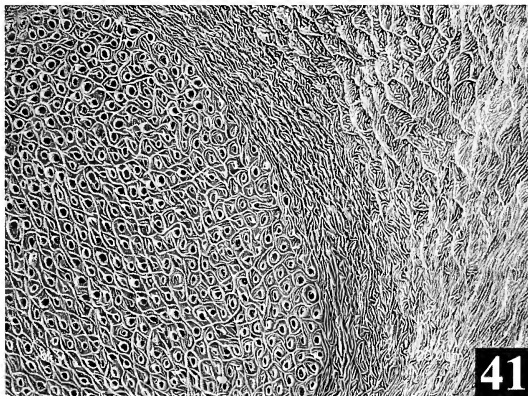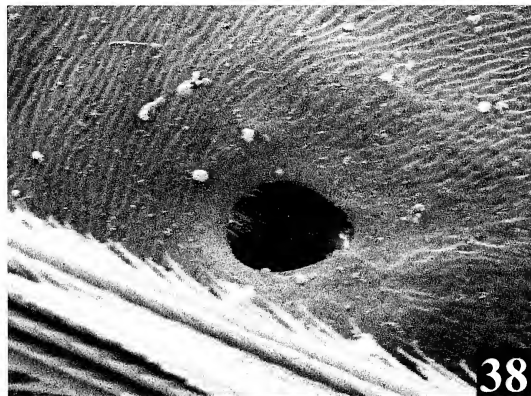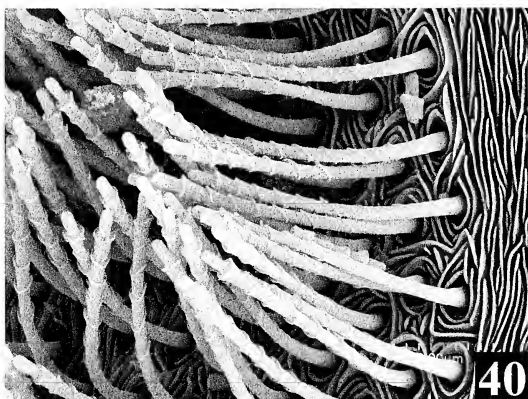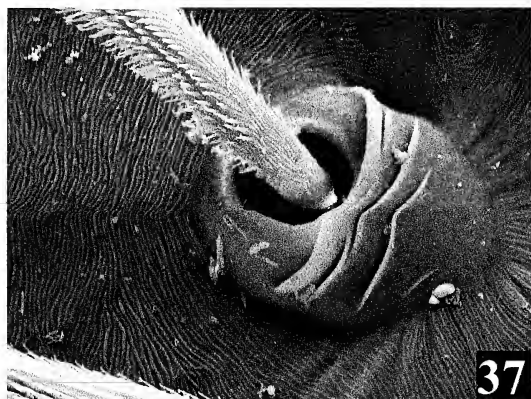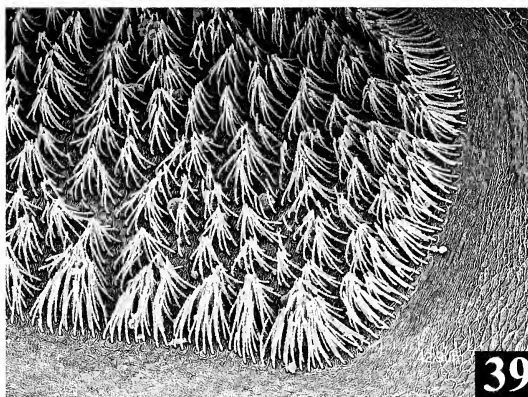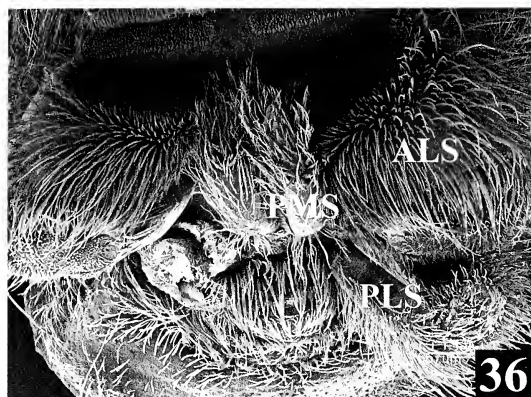
Figures 36–41.—*Psechrus tingpingensis.* 36. Female spinnerets, ventral view, without left PLS; 37. Trichobothrium; 38. Tarsal organ; 39. Female cribellum; 40. Female cribellum, enlarged; 41. Male cribellum.

the depressed epigynal median sclerite, the posteriorly enlarged copulatory ducts, the small spermathecae of female (Figs. 29, 30).

Female.—For body measurements, see Levi's (1982) description of female *P. sinensis.* White spot in front of cribellum present. Epigynal slits more or less parallel; epigynal median sclerite depressed, with width slightly longer than length; copulatory ducts apparent, widely separated, enlarged posteriorly; sper-mathecal heads apparent, situated mesally; spermathecae small, widely separated (Figs. 29, 30).

Male.—Unknown.

Other material examined. None.

Distribution.—China (Taiwan) (Map 3).

Psechrus tingpingensis Yin, Wang & Zhang
Figs. 31–47, Map 3

Psechrus tingpingensis Yin, Wang & Zhang 1985: 23, fig. 3 (female holotype and 2 female para-
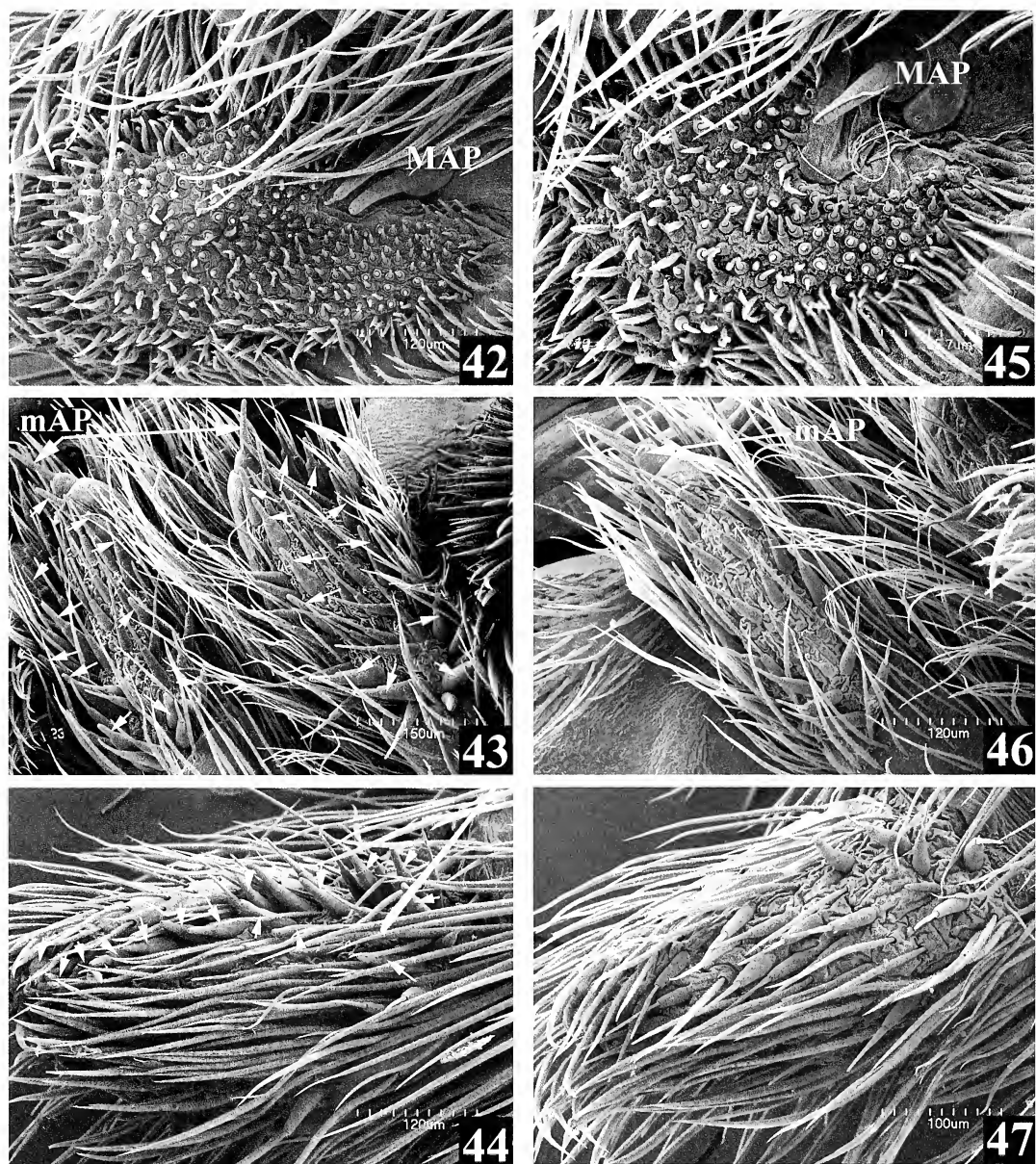
Figures 42–47.—*Psechrus tingpingensis*, spinnerets, ventral view. 42. Female, ALS, left; 43. Female, PMS, both; 44. Female, PLS, left; 45. Male, ALS, left; 46. Male, PMS, left; 47. Male, PLS, left (short arrows refer to cylindrical spigots; MAP refers to major ampullate spigots and mAP refers to minor ampullate spigots).

types from Tingping, Chenbu, Hunan, China, in HBI, examined). Song, Zhu & Chen 1999: 397, figs. 232I-J (male and female).

Diagnosis.—The male of this species is similar to *P. sinensis* and *P. senoculata* in having a rectangular embolic base and modified femur (Fig. 33), but can be recognized by the slightly bifid conductor apex, and the pres-

ence of two apophyses on embolic base (Figs. 31–33). The female of this species is similar to *P. sinensis* but can be distinguished by the much wider anterior part of epigynal median sclerite, and the anteriorly spiral copulatory ducts (Figs. 34, 35).

Male.—Total length 16.0–18.0. One medium-sized specimen measured: Total length

18.0. Carapace 8.0 long, 4.5 wide. Abdomen 10.0 long, 4.0 wide. Leg measurements: I: 62.1 (17.0, 20.0, 17.5, 7.6); II: 46.0 (14.0, 15.0, 12.0, 5.0); III: 28.0 (9.0, 8.5, 6.5, 4.0); IV: 45.2 (13.0, 14.0, 12.0, 6.2). White spot in front of cribellum present. Palpal femur modified; palpal bulb duct U-shaped; conductor long, bifid, with dorsal apophysis sharp, highly sclerotized, ventral one broad, membranous; conductor base not enlarged, but with numerous small tubercles; embolus short, broad with sharp apex; embolic base broad, with two strongly sclerotized apophyses (Figs. 31, 32).

Female.—Described by Yin, Wang & Zhang (1985). White spot in front of cribellum present. Epigynal slits approaching each other anteriorly; epigynal median sclerite wider posteriorly than anteriorly, with anterior part about ½ width of posterior part; copulatory ducts spiral anteriorly, widely separated posteriorly; spermathecal heads apparent, situated mesally; spermathecae rounded, widely separated (Figs. 34, 35).

Material examined.—CHINA: *Hunan:* Chengbu, Tingping, 31 July 1982, 1 female holotype and 2 female paratypes (J.F. Wang & Y.J. Zhang, HBI); Shimen, 25 June to 5 July 1992, 1 male and 2 females (X.J. Peng & L.P. Xie, HBI). *Guangxi:* Longsheng, 7 August 1982, 12 females (J.F. Wang & Y.J. Zhang, HBI); Ningming, May 1992, 1 male and 1 female (X. Pan, HBI); Ningming, 27 May 1997, 2 males and 2 females (Y.J. Zhang, HBI). **VIETNAM:** *Hanoi:* Tam Dao Mt. Forest Park, 2 May 1999, 2 males and 4 females (X.P. Wang, AMNH).

Distribution.—China (Hunan, Guangxi), Vietnam (Hanoi) (Map 3).

ACKNOWLEDGMENTS

LITERATURE CITED

Berland, J. & L. Berland. 1914. Description d'un *Psechrus* nouveau de Chine. Bulletin de la Societe entomologique de France 83:131–133.

Chamberlin, R.V. 1924. Descriptions of new American and Chinese spiders. Proceedings of the United States National Museum 63(13):1–38.

Chen, S.H. 1996. A checklist of spiders in Taiwan. Annual of Taiwan Museum 39:123–155.

Chen, X.E. & J.C. Gao. 1990. The Sichuan farmland spiders in China. Sichuan Science and Technology Publishing House, Chengdu, 226 pp.

Chen, Z.F. & Z.H. Zhang. 1991. Fauna of Zhejiang: Araneida. Zhejiang Science and Technology Publishing House, 356 pp.

Feng, Z.Q. 1990. Spiders of China in colour. Hunan Science and Technology Publishing House, 256 pp.

Hu, J.L. 1984. The Chinese spiders from the fields and the forests. Tianjin Press of Science and Techniques. 482 pp.

Lee, C.L. 1966. Spiders of Formosa (Taiwan). Taichung Junior Teachers College Publisher, 84 pp.

Lehtinen, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Annales Zoologici Fennici 4:199–468.

Levi, H.W. 1982. The spider genera *Psechrus* and *Fecenia* (Araneae, Psechridae). Pacific Insects, 24:114–138.

Murphy, J. 1986. Additional information concerning the spider family Psechridae. Bulletin of the British Arachnological Society 7:183–185.

Platnick, N.I. 1997. Advances In Spider Taxonomy 1992–1995, New York Entomological Society, 976 pp.

Platnick, N.I. 2000. The World Spider Catalog. American Museum of Natural History Web Document.

Pocock, R.I. 1900. Arachnida. Fauna of British India, Including Ceylon and Burma. London, 279 pp.

Song, D.X. 1987. Spiders From Agricultural Regions Of China (Arachnida: Araneae). Agriculture Publishing House, Beijing, 376 pp.

Song, D.X. 1988. A revision of the Chinese spiders described by Chamberlin. Sinozoologica 6:123–136.

Song, D.X., M.S. Zhu & J. Chen. 1999. The Spiders Of China. Hebei Science and Technology Publishing House, Shijiazhuang, 640 pp.

Thorell, T. 1881. Studi sur Ragni Malesi e Papuani III. Nel Museo Civico di Storia Naturale di Genova 17:1–720.

Thorell, T. 1895. Descriptive Catalogue Of The Spiders Of Burma. British Museum, London, 406 pp.

Thorell, T. 1897. Viaggio di Leonardi Fea in Birmania e regioni vicine. Nel Museo Civico di Storia Naturale di Genova 37:161–267.

Wang, J.F. 1990. A new species of psechrid spider from China (Aeaneae: Psechridae). Natural Science Journal of Hunan Normal University 13:257–258.

Xu, Y.J. & L. Wang. 1983. A record of *Psechrus mimus* Chamberlin. Journal of Huizhou Teachers College 2:35–36.

Yang, Z.L. & X.Z. Wang. 1993. A newly recorded of the spider genus *Fecenia* (Araneae: Psechridae) from China. Acta Arachnologica Sinica 2:27–28.

Yin, C.M., J.F. Wang & Y.J. Zhang. 1985. Study on the spider genera *Psechrus* from China. Journal of Hunan Teachers College (Natural Science Edition) 1:19–27.

Zhu, C.D. 1983. A list of Chinese spiders (revised in 1983). Journal of Bethune Medical University 9 (supplement): 1–130.

Zhang, Z.H., P.P. Yuan, F.P. Tong & Z.F. Chen. 1998. Study on fine structure of the two spider (Metathelae: Cribellatae). Journal of Hangzhou University 25(1):74–79.

A COMPARATIVE STUDY OF THE BIOLOGY AND KARYOTYPES OF TWO CENTRAL EUROPEAN ZODARIID SPIDERS (ARANEAE, ZODARIIDAE)

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ABSTRACT. A comparison of the biology and karyotypes of *Zodarion germanicum* and *Zodarion rubidum* (Araneae, Zodariidae) which occur in central Europe was carried out. Surprisingly, these species were found to differ in a number of characters such as pattern of activity, reproduction and karyotypes. *Zodarion germanicum* was observed to be diurnal, whereas *Z. rubidum* is nocturnal. Courtship and mating were markedly longer and more complex in *Z. germanicum* than in *Z. rubidum*. Females of *Z. germanicum* produced only one or two successive egg sacs including 17 eggs on average which they would guard, while females of *Z. rubidum* produced up to 5 egg sacs each having 4 eggs that they abandoned. The two species differ from each other also in number of chromosomes and the sex chromosome system. Results suggest these species belong to distant evolutionary lineages within the genus *Zodarion*.

Keywords: Araneae, Zodariidae, activity, reproduction, karyotype

About 500 species of Zodariidae have been described so far, most of which occur in the subtropical region (Jocqué 1991). In Europe, only one genus, *Zodarion*, including 47 species (Bosmans 1993, 1997), occurs. These species are well-known for being myrmecophagous and for constructing remarkable retreats from soil grains (e.g., Nielsen 1932). This remarkable behavior was observed for the first time more than 100 years ago (Simon 1864; Santschi 1908). Since then there have been seven studies concerning the biology of these spiders (Wiehle 1928, 1953; Schneider 1971; Harkness 1976, 1977a, b, 1995; Jocqué & Billen 1987; Couvreur 1990; Harkness & Harkness 1992). Nevertheless, a great majority of these investigations was centered upon the ant-eating behavior only. Thus, many other aspects of biology of these fascinating spiders, such as pattern of activity or reproduction, are poorly understood or even unknown.

In our study we focused on two species, *Zodarion germanicum* (C.L.Koch 1837) and *Zodarion rubidum* Simon 1914, the only representatives of the genus *Zodarion* in the Czech Republic and Slovakia. The former and larger species (body length 3.5–6.0 mm) oc-

curs abundantly in dry habitats associated with coniferous woodland only in central Europe. The latter and slightly smaller species (3–4 mm), was known only from southwestern France (Denis 1935). But in the last decades it has spread into central Europe, for example, onto sand dunes in South Moravia, Czech Republic (Pekár 1994). Both species show invasive tendencies as they often occur in secondary habitats. *Z. germanicum*, for instance, was recorded from heather rimming forested peat-bog (Mähringová 1993), and *Z. rubidum* on sandy substrates within the area of Berlin railway station (Germany) (Broen & Moritz 1987) or on mining dumps in Slovakia (Pekár 1994; Krajča 1996). At present, the ranges of the two zodariid species overlap in central Europe, but only in a few examples was sympatric occurrence proven at the ecological level (e.g., Jelínek 1999).

Based on morphological characters of copulatory organs, Bosmans (1997) classified 47 European species of the genus *Zodarion* into six groups. *Zodarion germanicum* was placed in "germanicum" while *Z. rubidum* was placed in "rubidum." At the beginning of our observations, the two species appeared to be

very similar, both occurring in identical habitats and foraging on similar ant species (Pekár unpubl. data). However, later investigation showed that these species mimic different ant species (Pekár & Král unpubl.) and have different activity. Thus our aim was to focus in detail on aspects of their biology which have been insufficiently studied in order to clarify differences between the study species which could have significance for further study of evolution within the genus *Zodarion*.

STUDY AREA

The study sites are situated in Slovakia which is in the center of the distribution of *Z. germanicum* and at the northeastern edge of the distribution of *Z. rubidum*.

Zodarion rubidum was observed on a mining dump in Nováky town. The dump (about 25 years old) consists of Tertiary tuff and coal slate and is sparsely covered with vegetation, dominated by the grass *Calamagrostis epigeios* (L.) Roth. *Zodarion germanicum* was observed on a steep outcropping in a nearby village Opatovce nad Nitrou, about 6 km from Nováky. This study area is a former sand pit adjacent to a pine forest (*Pinus silvestris* L.). It was abandoned some 15 years ago. The Neogene conglomerate sands of this site are mostly barren, with many stones and the cover is sparse vegetation dominated by the grass *Dactylis glomerata* L. The elevation of both sites is 275–290 m. The average annual temperature of the area is 8.5 °C, and the average annual precipitation is 650 mm. Average biweekly temperatures for the sites are displayed in Fig. 1. Soil surface temperature of the study areas was measured under a clear sky (on 7 and 8 June 1997) by means of a THERM 2246-2 thermometer at 0600, 1000, 1400 and 1800 h. Obtained data showed that the temperatures of study sites were very similar.

METHODS

The investigation took place both in the field and under laboratory conditions. From April to October 1997, weekly visits were made to the study areas to assess the proportion of adult spiders which were either running on the ground or hidden in retreats. On one day in June 1997, the number of both spider species (seen during 5 min) and the number of ants (seen during 30 sec) in a 1 m²

circle drawn in the soil around three nest entrances was assessed every hour (between 0600 and 2200 h). In June the sun rises at about 0445 h and sets at about 2045 h in the study area. The frequency of ant species hunted by spiders was also recorded in June. A few egg sacs (3 in *Z. rubidum* and 2 in *Z. germanicum*) were collected, and the sizes of eggs were measured using a stereoscopic microscope.

Forty adult individuals (20δ $20\female$) of each species were brought into the laboratory in June to investigate their behavior. The individuals were kept in specimen containers (diameter 15 mm, 60 mm long) at 20 °C ± 2° and under natural LD regime (14:10). They were offered various substrates, such as soil, sand grains, paper, pine needles, leaves, and other plant material, all potentially useful for the construction of retreats. The relative frequency and size of retreats constructed was measured after three days. The substrate was moistened as it dried out, usually at three-day intervals. The reared specimens were fed in excess with ant workers of *Tetramorium caespitum* (L.).

Then all 40 specimens were moved in pairs (male and female) to a Petri dish (diameter 60 mm) with a filter paper attached to the bottom, and kept separated by a paper barrier in order to study their reproductive behavior. As soon as the male began to "search," the barrier was removed. Style and duration of courtship and mating were observed under binocular stereomicroscope. After copulation males were removed. If the female was not receptive the males were immediately removed.

After females laid eggs, the number of egg sacs produced and the incubation periods were recorded. Individual fecundity was assessed by summing the number of hatched offspring with the number of undeveloped eggs which were left in each egg sac.

Data on the duration of mating, the number and size of eggs, and the incubation period for the two study species were compared using the permutation (exact) test since they did not meet the criteria required for parametric tests. A two-sided 2-sample randomization test after Manly (1997) was used. The simulation test procedure was constructed within RESAMPLING STATS program (Simon 1993).

Two different methods were used for chromosome preparations. The first method was
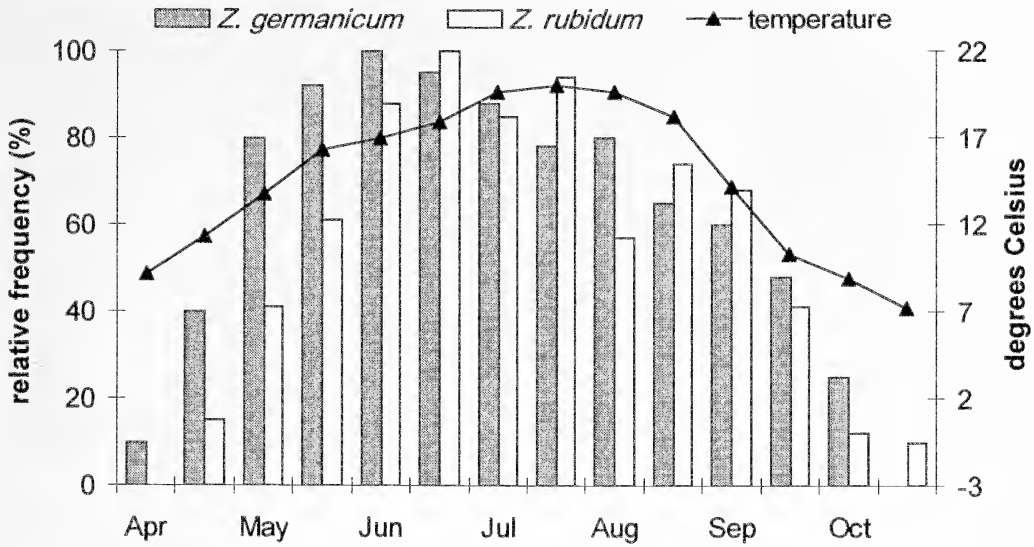
Figure 1.—Relative frequency of mature specimens of *Zodarion germanicum* and *Zodarion rubidum* compared with the average temperatures (▲) in the study region at biweekly intervals.

used for preparation of chromosomes from subadult and adult individuals. The entire contents of the abdomen were dissected out in a hypotonic solution (0.075 M KCl). After 20–25 min of hypotonic treatment, the tissues were placed into a small beaker with fresh fixative (a mixture of absolute methanol and glacial acetic acid, 3:1). The pieces of the tissues were incubated in a beaker in a refrigerator at 5 °C. During the first hour of incubation, the fixative was renewed twice (after 15 and 45 min of incubation). After 5–6 h the tissues were placed into a tube with new fixative, resuspended, and centrifuged at 2000 G for 5 min. The supernatant was discarded and the sediment was diluted in fresh fixative to an optimal concentration of fixed cells. The suspension was then dropped onto clean slides.

The chromosomes from first instar specimens were obtained by a modification of the spreading technique used by Traut (1976) as follows. The entire contents of the abdomen were dissected out and treated in hypotonic solution as in the former case. Following a 15–30 min fixation in freshly prepared Carnoy fixative (ethanol:chloroform:glacial acetic acid 6:3:1) the tissue was placed in a drop of 60% acetic acid on a clean slide. The tissue was quickly shredded as finely as possible with a pair of fine tungsten needles. The slide was then placed quickly on a warm histological plate (surface temperature of 40 °C) and

the drop of dispersed tissue was allowed to evaporate while keeping it moving constantly using a fine tungsten needle.

The slides obtained by both methods were air-dried at room temperature overnight, and stained with 5% Giemsa solution in Sörensen phosphate buffer (pH = 6.8) for 5–6 min (Cokendolpher & Brown 1985).

RESULTS

Phenology.—The phenology diagrams for the study species are shown in Fig. 1. Seasonal activity of spiders began in April when both juvenile and subadult specimens appeared on the ground and started hunting. Of the *Z. germanicum* specimens collected on 25 April 1997, 40% (*n* = 15) were adult, increasing to 80% (*n* = 25) within two weeks (11 May 1997). During that time, all individuals of *Z. rubidum* (*n* = 17) were still subadult. On 25 May 1997 92% (*n* = 24) of specimens of *Z. germanicum* and 61% (*n* = 31) of *Z. rubidum* were adult. In 1997, mating began in April (*Z. germanicum*) or at the end of May (*Z. rubidum*). The egg sacs were found on 17 June 1997. Examining cocoons the first free instar was found on 2 July for *Z. germanicum* and on 19 July for *Z. rubidum*. The last adults were recorded on 2 October for *Z. germanicum* and on 30 October for *Z. rubidum*. Both species overwinter as juveniles hiding in retreats.
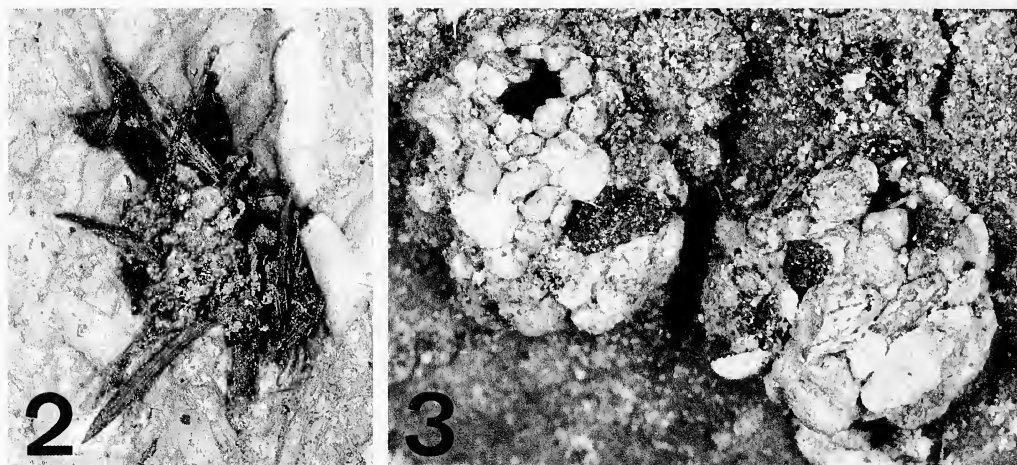
Figures 2, 3.—Igloo-shaped retreats. 2. *Zodarion germanicum* on the lower surface of a stone, constructed of soil and pine needles; 3. *Zodarion rubidum*, constructed of sand grains and attached to the lower surface of a stone.

Shelters.—The spiders rest and molt in retreats (Fig. 2). The retreats are closed solitary "igloo-shaped" shelters, usually attached to a solid substrate, such as the lower surface of stones, usually near an ant nest entrance. Often an aggregation of retreats attached to a stone was found (Fig. 3). In the field, the retreats were constructed with a wide variety of materials (e.g., soil or sand grains, plant material, pine needles) held together by webbing. In the laboratory, the retreats were also constructed of artificial material, e.g., paper. A new retreat was constructed when the old one was destroyed, or after molting. The material was collected by a spider from the vicinity of a retreat site. A spider brought a particle in its palps to a certain place, held it by a leg IV, attached it to the substrate with silk, and then continued this process until the retreat was complete. The construction of retreats lasted 0.5–2 h, depending on the availability of a suitable material. Nevertheless, in the laboratory 45% ($n = 40$) of specimens of *Z. germanicum* and 38% ($n = 40$) of *Z. rubidum* did not construct a retreat within 3 days. Such behavior was observed also in the field, where many individuals did not construct a retreat and were found to rest in soil holes or rock crevices and in other similar shelters. The diameter of retreats constructed by *Z. germanicum* was on average 5.6 ± 0.2 (S.D.) mm ($n = 8$) for adult males, 9.4 ± 0.2 mm ($n = 10$) for adult females and 4.1 ± 0.1 mm ($n = 12$) for the first instar. In *Z. rubidum* it was on

average 4.8 ± 0.2 mm ($n = 6$) for adult males, 5.3 ± 0.1 mm ($n = 9$) for adult females and 3.0 ± 0.1 mm ($n = 10$) for the first instar spiders. When no suitable material was offered, females usually spun a small sheet web (about 1 cm^2) to hide under, whereas males did not construct such a web.

Activity.—*Zodarion germanicum* was found to be active during the day. In June its activity began at about 0700 h and terminated approximately at 2100 h. The spiders were seen hunting and mating near the entrances of ant nests during all activity period, but before sunset they moved into an old retreat or constructed a new one. There was a slight decline in activity between 1000 h and 1400 h when the temperature of soil surface reached 40 °C and the ants were most active (Fig. 4). During rainy or cool days (i.e., average day temperature about 15 °C), the number of active spiders was approximately halved. Individuals of *Z. rubidum* were active in the morning (0600–0900 h) and in the evening (1830–2200 h) (Fig. 5). There was no spider active between 1000–1700 h. The nocturnal activity of this species was not investigated. The spiders were hunting and mating during both periods of activity; construction of retreats was recorded only in the evening. During these periods the surface temperature fell below 30 °C.

Courtship and mating.—When a male of *Z. germanicum* approached a female, it began to move very slowly with the whole body vibrating, with waving raised forelegs and
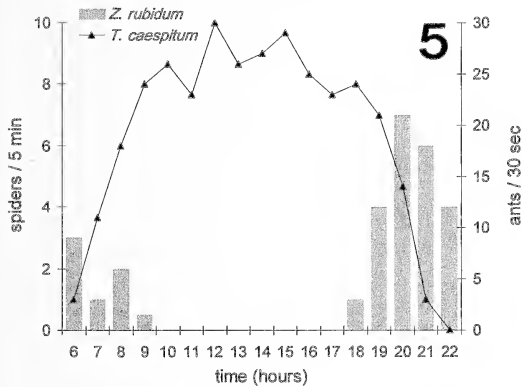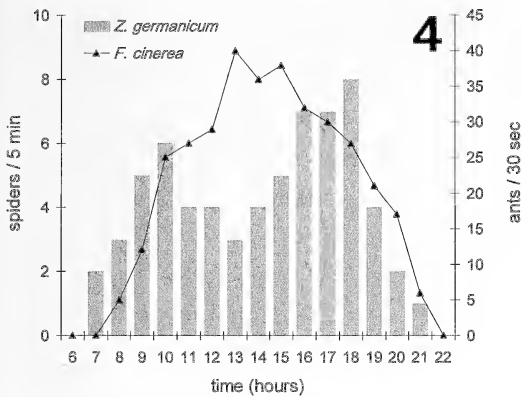
Figures 4, 5.—Activity (mean number, $n = 3$) of spiders compared to the activity of ant species which the spiders most frequently hunted. 4. *Zodarion germanicum* and *Formica cinerea* in Opatovce nad Nitrou; 5. *Zodarion rubidum* and *Tetramorium caespitum* in Nováky.

drumming palps. When reaching a female, the male first lightly touched her with his forelegs, then followed by a "sparring" with palps. If the female was receptive she became passive, stayed in a normal position; and the male, still vibrating, moved across her and inserted palpal organs first from one side, then from the other side. This mating position is

classified by Foelix (1996) as 'type 3.' The courtship of *Z. rubidum* was much shorter. The male quickly approached the female with twitching raised forelegs and drumming palps. After a short period of palpation, they copulated in the same way as in *Z. germanicum*. The copulation lasted on average 11.9 ± 0.3 (S.D.) min ($n = 18$) in *Z. germanicum*, and 1.3 ± 0.1 min ($n = 15$) in *Z. rubidum*. The difference in duration is highly significant ($P < 0.001$; 2-sample randomization test, 4999 simulations). Soon after this primary, "long" copulation, the female of both species could copulate again with another male but the subsequent mating (which involved attempts to insert a palp from each side) lasted less than 15 sec. Before and after such short mating the female was vibrating/quivering.

Fertility and brood care.—The eggs were laid in woolly silken sacs (Fig. 6). There were on average only 4.2 eggs in a cocoon of *Z. rubidum* but 16.5 eggs in a cocoon of *Z. germanicum* (Table 1). The difference in number of eggs between the species is highly significant ($P < 0.001$; 2-sample randomization test, 4999 simulations). The eggs of both species were cream-colored and did not stick to each other but rolled freely. The mean diameter of eggs was 0.79 in *Z. rubidum* and 0.9 mm in *Z. germanicum*. The eggs of *Z. germanicum* were significantly larger ($P < 0.001$; 2-sample randomization test, 4999 simulations) than those of *Z. rubidum*.

Females of *Z. rubidum* produced an egg sac on average within 9 days after copulation whilst females of *Z. germanicum* produced an egg sac on average within 14 days (Table 1). Females of *Z. rubidum* produced up to 5 egg sacs within a month while females of *Z. germanicum* produced one or (in one case) two successive egg sacs, after hatching offspring from the first one. The female of *Z. rubidum* hid each egg sac in a separate retreat and kept on hunting ants without paying attention to

Table 1.—Comparison of differences (mean ± standard deviation) found in the reproduction of the two study species.

	Z. rubidum	Z. germanicum
Number of eggs/cocoon	4.2 ± 0.1 ($n = 13$)	16.5 ± 0.3 ($n = 15$)
Diameter of eggs (mm)	0.79 ± 0.01 ($n = 12$)	0.9 ± 0.01 ($n = 24$)
Time to egg sac production (days)	5–13 ($n = 13$)	2–26 ($n = 15$)
Incubation period (days)	57.5 ± 1.1 ($n = 9$)	39.6 ± 1.9 ($n = 5$)
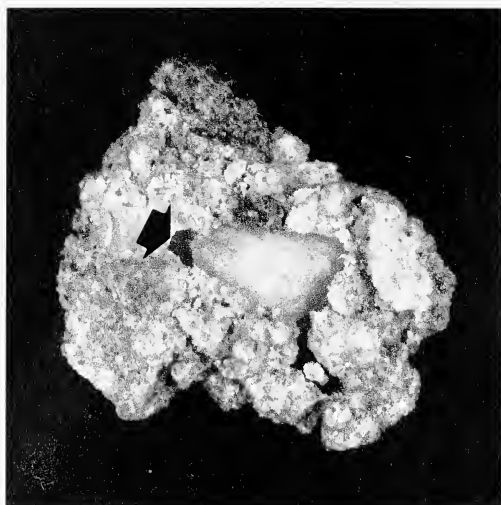
Figure 6.—Retreat of *Zodarion rubidum* including remnants of cocoon. Arrow points to the opening which spiderlings used to escape. The cocoon is the smooth-surfaced structure at the center.

the cocoons except for placing an occasional (31%, $n = 13$) dead ant in the retreat containing an egg sac. In contrast, the female of *Z. germanicum* built a large retreat in which the egg sac was placed and stayed on guard inside. She left the retreat approximately once during a four-day period to feed.

The first instar emerged from the egg sac on average 57.5 days after laying eggs in *Z. rubidum*, and after 39.6 days in *Z. germanicum* (Table 1). Nevertheless, the difference in the incubation period is not significant ($P = 0.17$; 2-sample randomization test, 4999 simulations). In the laboratory, the female of *Z. germanicum* died at last, and was fed upon by some of the first instar spiders. Spiderlings stayed in the remains of the cocoon until the first molt, which occurred within a few days of emergence. They then dispersed from the cocoon through a tiny opening on the side without assistance of the female (Fig. 6), and each specimen constructed its own tiny retreat.

Karyotype.—Both mitotic and meiotic phases were obtained from subadult and adult males. The first instar and females gave only mitotic phases. Acrocentric chromosomes predominated in karyotypes of the both species but differences in the size of particular chromosomal pairs were apparent. The diploid chromosome number (2n) in *Z. germanicum* was 29 for males (Figs. 8, 10), and 30 for females and in *Z. rubidum* 24 for males (Figs. 7, 9), and 26 for females. The comparison of meiotic male phases with mitotic metaphases of both sexes indicated an X0 type of sex chromosome system in *Z. germanicum*, with male X0 and female XX. The large X chromosome was acrocentric. *Z. rubidum* possesses sex chromosome system $X_1X_2$0 with male X_1X_2 and female $X_1X_1X_2X_2$. Both X chromosomes were acrocentric but of different size. Similar to the majority of spiders analyzed so far, the X chromosome(s) in males of both species show greater condensation than autosomes during prophase I (positive heteropycnosis) and lie on the periphery of meiotic figures until metaphase II. In *Z. rubidum*, both X chromosomes are aligned closely to each other, not only during the first meiotic division, like the majority of species of spiders analysed so far, but even until metaphase II.

DISCUSSION

Because both species belong to the same genus, we expected that they might have similar life histories. Surprisingly, besides some similarities we also found several striking differences. Both species construct, like other species of the genus *Zodarion* studied so far, 'igloo-shaped' retreats. Observed building procedure was in agreement with the one given by Harkness (1977b) and Couvreur (1990). From an evolutionary point of view, we suppose the retreats are an apomorphy derived from simple burrowing behavior known from many other zodariid groups (Jocqué 1991) used for protection in an unusual environment of ground-living ants. Surprisingly, the construction of the retreats does not seem to be an obligatory habit of all specimens, as suggested by both laboratory and field observations. However, we suppose that even hiding in soil or in other similar places could be considered as a remnant of burrowing behavior.

Couvreur (1990) described two types of retreats, open and closed, constructed by *Z. rubidum*. According to him, the spiders hide in the open retreats when hunting but use closed retreats when resting. We have never observed open retreats either in a field or in a lab. In contrast to the laboratory findings of Harkness (1977b) on *Z. frenatum* Simon, we did not observe marked differences between the number of males and females which constructed retreats.
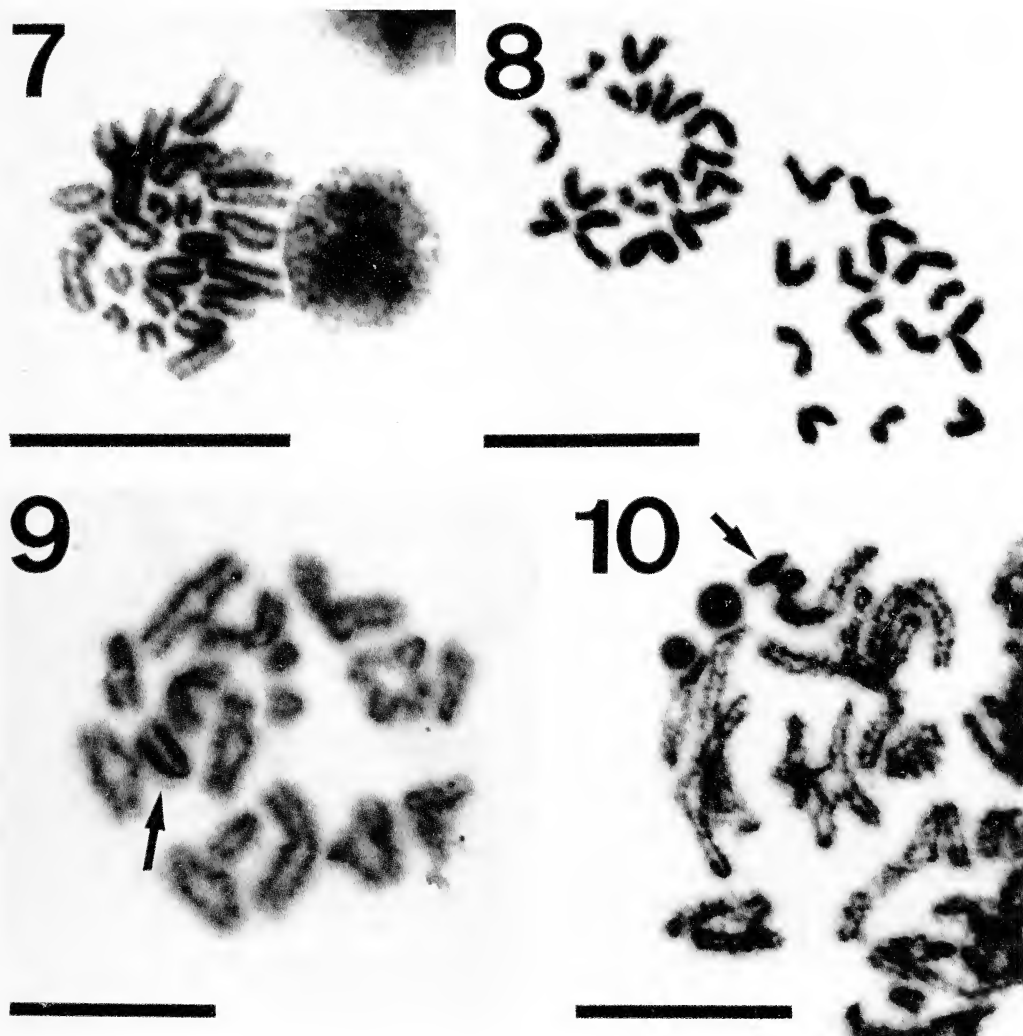
Figures 7–10.—7. *Zodarion rubidum*, mitotic metaphase of male; 8. *Zodarion germanicum*, two male daughter cells at metaphase II. Note differences in the size of particular chromosomes, especially in *Zodarion rubidum*; 9. *Zodarion rubidum*, diplotene of male; 10. *Zodarion germanicum*, diplotene of male. Arrow points to X chromosome(s) displaying still weak positive heteropycnosis. Scale line = 0.01 mm.

The onset of activity and maturity of *Z. rubidum* was delayed in comparison with *Z. germanicum* by about two weeks within which period the average temperature increased about 5 °C. This delay might be a consequence of the fact that the former species has spread to central Europe from southern Europe where the average day temperatures are considerably higher. The activity patterns of both species were clearly different. We observed *Z. rubidum* to be active in the evening and in the morning. We did not investigate its activity during the night since Couvreur (1990) studied the nocturnal activity of this

species in detail. Nocturnal activity was found also in other species of the genus *Zodarion*: *Z. frenatum* Simon 1884 (Harkness 1977a) and *Zodarion* sp. from Afghanistan (Schneider 1971). On the contrary, diurnal activity as observed in *Z. germanicum* has never been reported for any species of the genus *Zodarion*.

Until now, information gathered about mating and related behavior of the genus *Zodarion* has been very scarce and incomplete. Our observation revealed that although both species copulated in the same position, characteristic for "modern" wandering spiders (Foelix 1996), significant differences in courtship

and mating were observed. In *Z. germanicum*, courtship and mating took more time and were more complex than in *Z. rubidum*.

Except for the "long" copulation that we consider a true one, we also recorded multiple short copulations in both species. Such copulations were also noticed by Gerhardt (1928) who observed in *Z. elegans* (Simon 1873) multiple copulations, each lasting only a few sec. We consider this a pseudo-copulation. After the true copulation, the females became unreceptive and expressed this by a specific behavior (quivering) which threatened the male. A similar behavior was observed for the female of a thomisid spider, *Xysticus cristatus* (Clerck 1757) (Bristowe 1941).

Females of both species hid their egg sacs in retreats as observed by Harkness (1995) in *Z. frenatum* but showed different brood-care strategies. While females of *Z. germanicum* produced only one or two egg sacs of approximately 16 eggs each and guarded the egg sacs, females of *Z. rubidum* produced on average 5 egg sacs of approximately 4 eggs, and exhibited no further care. Wiehle (1953) found 25–50 eggs per egg sac in *Z. germanicum*. However, we found a maximum of 25 eggs per egg sac of this species. Regarding other *Zodarion* species, Harkness (1995) reported 9–12 eggs/egg sac of *Z. frenatum*. Unfortunately, he did not mention either how many egg sacs the female produced or whether the female guarded the egg sacs or not.

With respect to the karyology, the family Zodariidae appears to be practically an unknown group. Only one short note on the number of chromosomes in "*Storena*" *indica* Tikader & Patel 1975 (2n, male = 22; X_1X_20) has been published (Datta & Chatterjee 1983). Males of the species examined possess a haploid number of chromosomes which is close to the mean male haploid number of chromosomes ($n = 14.09$) in spiders (Gowan 1985). Though both species studied are placed in the same genus, they differ considerably in the number of chromosomes as well as in the sex chromosome system. From an evolutionary point of view, *Z. rubidum* exhibited a sex chromosome system that seems to be an ancestral trait in spiders (Suzuki 1954; White 1973). This sex chromosome system was also found in the most primitive recent spider taxon, i.e., in Mesothelae (Suzuki 1954). Thus we hypothesize that the system X0 in *Z. ger-*

manicum is derived from the X_1X_20. The large acrocentric X chromosome of this species might have originated by tandem fusion between the ancestral acrocentric chromosomes X_1 and X_2 that are still conserved in the karyotype of "*S.*" *indica* and *Z. rubidum*.

Our comparative study revealed that although both species are placed in the same genus, they differ in a number of characters such as activity pattern, courtship, mating, brood care, karyotype and sex chromosome system. Our results support Bosman's (1997) separation of these species into two different groups and suggest they might belong to distant evolutionary branches of this genus. However, to understand further the evolution process within the genus *Zodarion*, we suggest additional research of these aspects of biology in other representatives of this genus. We assume such investigation might also contribute a clarification of the evolution of mimicry in the subfamily Zodariinae.

ACKNOWLEDGMENTS

LITERATURE CITED

Bosmans, R. 1993. Revision of the genus *Zodarion* Walckenaer, 1833 in the Iberian peninsula and Balearic islands (Araneae, Zodariidae). Eos 69: 115–142.

Bosmans, R. 1997. Revision of the genus *Zodarion* Walckenaer, 1833, part II. Western and central Europe, including Italy (Araneae: Zodariidae). Bulletin of the British Arachnological Society 10:265–294.

Bristowe, W.S. 1941. The Comity of Spiders. II. Ray Society, London.

Broen von, B. & M. Moritz. 1987. Zum Vorkommen von *Zodarion rubidum* (Simon, 1914) im Berliner Gebiet. Deutsche Entomologische Zeitschrift 34:155–159.

Cokendolpher, J.C. & J. Brown. 1985. Air-dry method for studying chromosomes of insects and arachnids. Entomological Newsletter 96:114–118.

Couvreur, J.M. 1990. Quelques aspects de la biologie de *Zodarion rubidum*, Simon, 1914. Nieuwsbrief van de Belgische Arachnologische Vereniging 7:7–15.

Datta, S.N. & K. Chatterjee. 1983. Chromosome number and sex determining mechanism in fifty-two species of spiders from north-east India. Chromosome Information Service 35:6–8.

Denis, J. 1935. A propos de quelques Araigneés du genre *Zodarion* Walck., appartenant á la faune française. Bulletin de la Societe d'Histoire Naturelle de Toulouse 67:51–68.

Foelix, R.F. 1996. Biology of Spiders, 2nd ed. Oxford University Press, New York.

Gerhardt, U. 1928. Biologische Studien an griechischen, corsischen und deutschen Spinnen. Zeitschrift für Morphologie und Ökologie der Tiere 10:576–675.

Gowan, T.D. 1985. The life history and reproduction of the wolf spider *Lycosa lentia* Hentz. Dissertation, University of Florida, Gainesville.

Harkness, R.D. 1976. The relation between an ant, *Cataglyphis bicolor* (F.) (Hymenoptera: Formicidae) and a spider, *Zodarion frenatum* (Simon) (Araneae: Zodariidae). Entomologist's Monthly Magazine 111:141–146.

Harkness, R.D. 1977a. Further observations on the relation between an ant, *Cataglyphis bicolor* (F.) (Hymenoptera: Formicidae) and a spider, *Zodarion frenatum* (Simon) (Araneae: Zodariidae). Entomologist's Monthly Magazine 112:111–123.

Harkness, R.D. 1977b. The building and use of "shelters" by a hunting spider (*Zodarion frenatum* Simon) in Greece. Zoologischer Anzeiger 199:161–163.

Harkness, R.D. 1995. The use of "shelters" by an ant hunting spider, *Zodarium frenatum* Simon, as receptacles for eggs. Entomologist's Monthly Magazine 131:46.

Harkness, M.L.R. & R.D. Harkness. 1992. Predation of an ant (*Cataglyphis bicolor* (F.) Hym., Formicidae) by a spider (*Zodarium frenatum* (Simon) Araneae, Zodariidae) in Greece. Entomologist's Monthly Magazine 128:147–156.

Jelínek, A. 1999. Výskyt teplomilných druhů pavouků (Araneae) v údolí řeky Jihlavy na Českomoravské vrchovině [Occurrence of thermophilous spiders (Araneae) in the valley of the river Jihlava in Českomoravská vrchovina]. M.Sc. thesis, Charles University, Prague.

Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201:1–160.

Jocqué, R. & J. Billen. 1987. The femoral organ of the Zodariinae (Araneae, Zodariidae). Revue de Zoologie Africaine 101:165–170.

Krajča, A. 1996. Spoločenstvá pavúkov (Araneae) na niklových haldách v Seredi [Spider communities of nickel dumps in Sered, Slovak Republic]. M.Sc. thesis, Commenius University, Bratislava.

Manly, B.F.J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. Chapmann & Hall, London.

Mähringová, M. 1993. Střevlíkovití brouci (Col.: Carabidae) a pavouci (Araneida) různých typů rašeliništ' CHKO Třeboňsko [Carabid beetles and spiders of various peat-bogs in protected area of Třeboňsko, Czech Republic]. M.Sc. thesis, Charles University, Prague.

Nielsen, E. 1932. The Biology of Spiders, With Special Reference to the Danish Fauna. Levin & Munskgaard, Copenhagen.

Pekár, S. 1994. The first record of *Zodarion rubidum* and *Ostearius melanopygius* for Slovakia (Araneae: Zodariidae, Linyphiidae). Entomological Problems 25:97–100.

Santschi, F. 1908. Quelques observations nouvelles et remarques sur la variabilité de l'instinct de nidification chez les fourmis. Journal für Psychologie und Neurologie 13:136–149.

Schneider, P. 1971. Ameisenjagende Spinnen (Zodariidae) an *Cataglyphis*-Nestern in Afghanistan. Zoologischer Anzeiger 187:199–201.

Simon, E. 1864. Histoire naturelle des araignées (Aranéides). Paris.

Simon, J.L. 1993. Resampling: The New Statistics. 2nd ed. Resampling Stats, Wadsworth.

Suzuki, S. 1954. Cytological studies in spiders III. Studies on the chromosomes of fifty-seven species of spiders belonging to seventeen families with general considerations on chromosomal evolution. Journal of Science of the Hiroshima University (B) 15:23–136.

Traut, W. 1976. Pachytene mapping in the female silkworm *Bombyx mori* L. (Lepidoptera). Chromosoma 58:275-284.

White, M.J.D. 1973. Animal Cytology and Evolution. Cambridge University Press, Cambridge.

Wiehle, H. 1928. Beiträge zur Biologie der Araneen insbesondere zur Kenntnis des Radnetbaues. Zeitschrft für Morphologie und Ökologie der Tiere 11:115–151.

Wiehle, H. 1953. Zodariidae. Pp. 47–52. *In* Die Tierwelt Deutschland 42. (F. Dahl, ed.). Gustav Fischer Verlag, Jena.

UNDER THE INFLUENCE: WEBS AND BUILDING BEHAVIOR OF *PLESIOMETA ARGYRA* (ARANEAE, TETRAGNATHIDAE) WHEN PARASITIZED BY *HYMENOEPIMECIS ARGYRAPHAGA* (HYMENOPTERA, ICHNEUMONIDAE)

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ABSTRACT. On the evening that it will kill its host, the orb-weaving spider *Plesiometa argyra,* the larva of the ichneumonid wasp *Hymenoepimecis argyraphaga* induces the spider to perform highly stereotyped construction behavior and build an otherwise unique "cocoon web" that is particularly well-designed to support the wasp larva's cocoon. Cocoon web construction behavior is nearly identical with the early steps in one subroutine of normal orb construction, and is repeated over and over. Usually all other normal orb construction behavior patterns are completely or nearly completely repressed. Experimental removal of the larva one or a few hours before cocoon construction would normally occur is sometimes followed by nearly normal cocoon web construction, and sometimes by construction of other highly altered web designs. The mechanism by which the larva induces these changes in the spider's behavior is thus apparently a fast-acting chemical, with effects that are manifested gradually. Partial recovery of orb designs sometimes occurred several days later.

Keywords: Parasite, manipulation of host behavior, orb construction behavior, *Plesiometa, Hymenoepimecis*

Manipulation of host behavior by parasites is a widespread phenomenon (Holmes & Bethel 1972; Moore 1984; Barnard & Behnke 1990; Toft et al. 1991; Godfray 1994; McLachlin 1999; Poulin 2000), but most reports of behavioral modifications, especially those caused by insect parasitoids in other insects, involve only simple behavior patterns such as movement from one habitat to another, adoption of sleeping postures, or eating more or less (Wickler 1976; Godfray 1994; McLachlan 1999). Spider behavior is also influenced by insect parasitoids (Schlinger 1987). At least some of these changes may be due to relatively simple mechanisms, such as modification of particular receptors (Jenni et al. 1980). This report concerns an unusually selective behavioral modification by the larva of the parasitoid wasp *Hymenoepimecis argyraphaga* Gauld (Ichneumonidae), which apparently chemically induces expression of the early steps of one subroutine of orb web construction in the spider *Plesiometa argyra* (Walckenaer 1841) (Tetragnathidae), while suppressing all the rest of orb construction behavior (Eberhard 2000a). It may be the

most finely directed alteration of host behavior ever attributed to an insect parasitoid.

It has long been known that psychotropic substances can modify the forms of orb webs (Witt et al. 1968), but the details of how particular steps of the spider's construction behavior are affected have never been determined. Elucidation of which aspects of behavior are changed can have important consequences for the common use of details of building behavior as taxonomic characters (Eberhard 1982; Hormiga et al. 1995; Griswold et al. 1998), as well as how evolutionary transitions may have occurred. It has not always been clear whether or not some variant behavior patterns should be recognized as separate traits (Eberhard 1990). If particular behavior patterns can be selectively induced, then the case for their independence from other traits, and thus their potential usefulness as characters, is strengthened. Clarification of the behavioral effects of this wasp parasite on web construction behavior thus promises to improve understanding of the organization of behavior within the spider, and of the usefulness of different behavioral characters in spider taxonomy.

The life cycle of *H. argyraphaga* is the following (Eberhard 2000b). The female wasp attacks *P. argyra* as the spider rests at the hub of its orb, stings it into a temporary (10–15 min.) paralysis, and glues an egg to the spider's abdomen. Subsequently the spider resumes normal activity, and builds apparently normal orbs to capture prey during the next approximately 7–14 days while the wasp's egg hatches and the larva grows. The larva remains attached to the surface of the abdomen, and feeds by sucking hemolymph through small holes it makes in the spider's abdominal cuticle. The second instar larva, on the night that it will kill its host, induces the spider to construct an otherwise unique "cocoon web" of dragline silk, molts to the third instar, and then kills and consumes the spider. The next evening the larva spins a cocoon hanging by a line from the cocoon web. The larva (which is barely visible through the thin walls of the cocoon) pupates about 4 days later, and then emerges as an adult wasp after about 7 more days.

METHODS

Field observations were made near Parrita, Puntarenas Province, Costa Rica (elev. 10 m) in January and February of 1999 and 2000 in a mature plantation of African oil palm (*Elaeis guineensis* L.) where spider populations were dense. Web measurements were performed in the morning, and thus did not include webs built later in the day (which may have different designs—Eberhard 1988). Construction of cocoon webs made by spiders carrying wasp larvae was observed indoors near Parrita the night after the spiders were collected and transferred onto silk lines from *P. argyra* orbs that had been fastened to approximately horizontal 0.6 m dia. circular wire frames that were hung about 1 m above the floor. Larvae, which would kill their hosts that evening, could be reliably distinguished (15 of 15 cases) from others on the morning and afternoon of the same day, due to their larger size. Voucher specimens of wasps and spiders have been deposited in the U. S. National Museum of Natural History, the Museum of Comparative Zoology at Harvard, and the Museo de Entomología of the Universidad de Costa Rica.

The behavior of spiders from which the larva had been experimentally removed was ob-
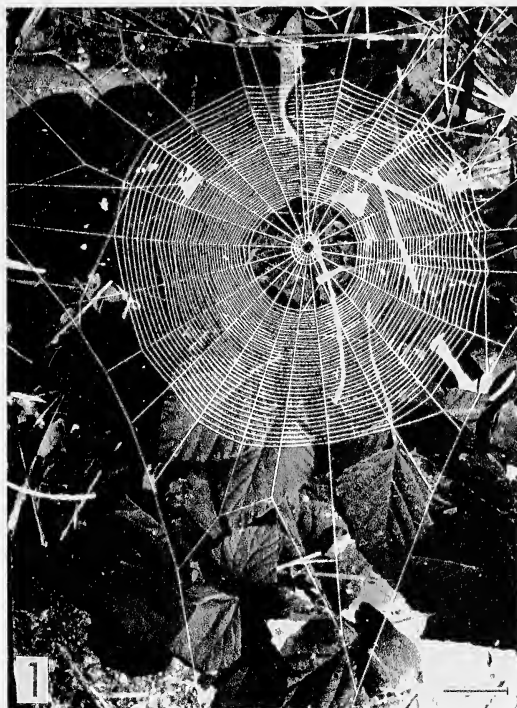
Figure 1.—Web of an unparasitized adult *Plesiometa argyra*. Scale bar = 3.0 cm.

served after the spiders had been taken to San Antonio de Escazu (elev. 1300 m), where they were kept indoors at room temperature for up to two weeks. On the evening the larva was to be removed, the spider was kept in a small container (6 cm dia.) in which it could not spin a web, and then placed on a wire frame as soon as the larva was removed between 2100 and 0200 h. Because the spiders seemed to need air movement to induce web construction, they were not kept in cages, but allowed to range freely in rooms.

RESULTS

Field.—The orbs of spiders carrying wasp eggs and larvae were not distinguishable from the more or less horizontal, moderately open-meshed orbs of unparasitized spiders (Figs. 1, 2) (ANCOVA analyses showed no significant effects of parasitism by larvae, or by eggs and larvae ($P = 0.91$, 0.40). Even parasitized spiders found the morning of the day on which they would be killed by the wasp larva were on freshly made, apparently normal orbs. Other than orbs, the only other webs on which unparasitized spiders occurred were small molting webs (Eberhard et al. 1993). These
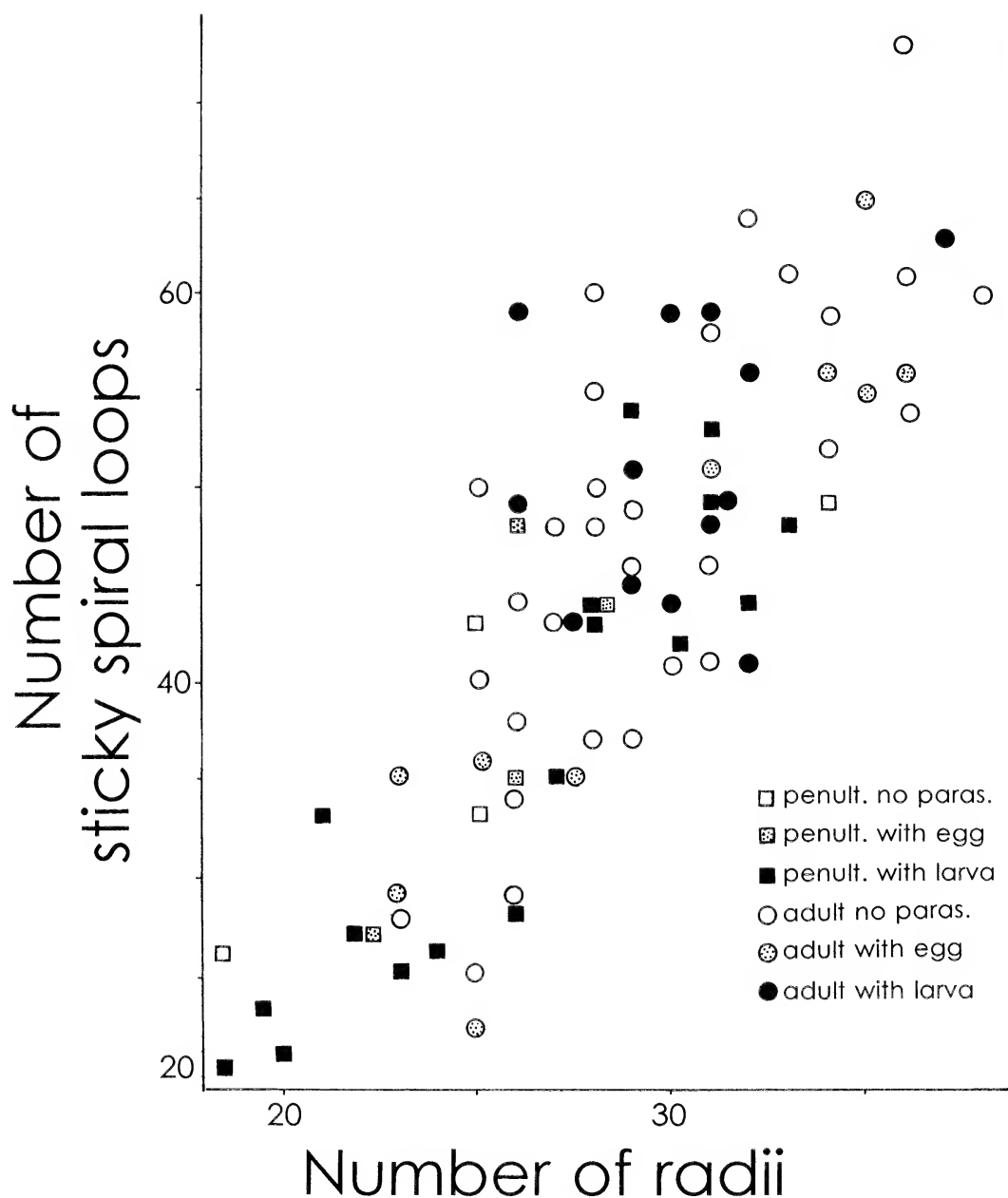
Figure 2.—Numbers of radii and sticky spiral loops (mean number of loops directly above, below, and to the sides of hub) in webs of spiders in the field that were parasitized (filled symbols) and unparasitized (open symbols). No differences between parasitized and unparasitized individuals were apparent.

webs were rare, and several newly molted individuals lacked such webs. Despite the dense spider populations, no egg sacs or webs associated with egg sacs were seen; egg sacs may be hidden in leaf litter, as in the closely related *Leucauge mariana* (Keyserling) (Ibarra et al. 1991; V. Mendez pers. comm.).

More than 100 cocoon webs were observed in the field. They almost always consisted of a few lines that radiated in a more or less horizontal plane from a "hub" or central area, where the cocoon's suspension line was attached, and were each attached directly to a support (Eberhard 2000a, Figs. 3–5). Most ra-
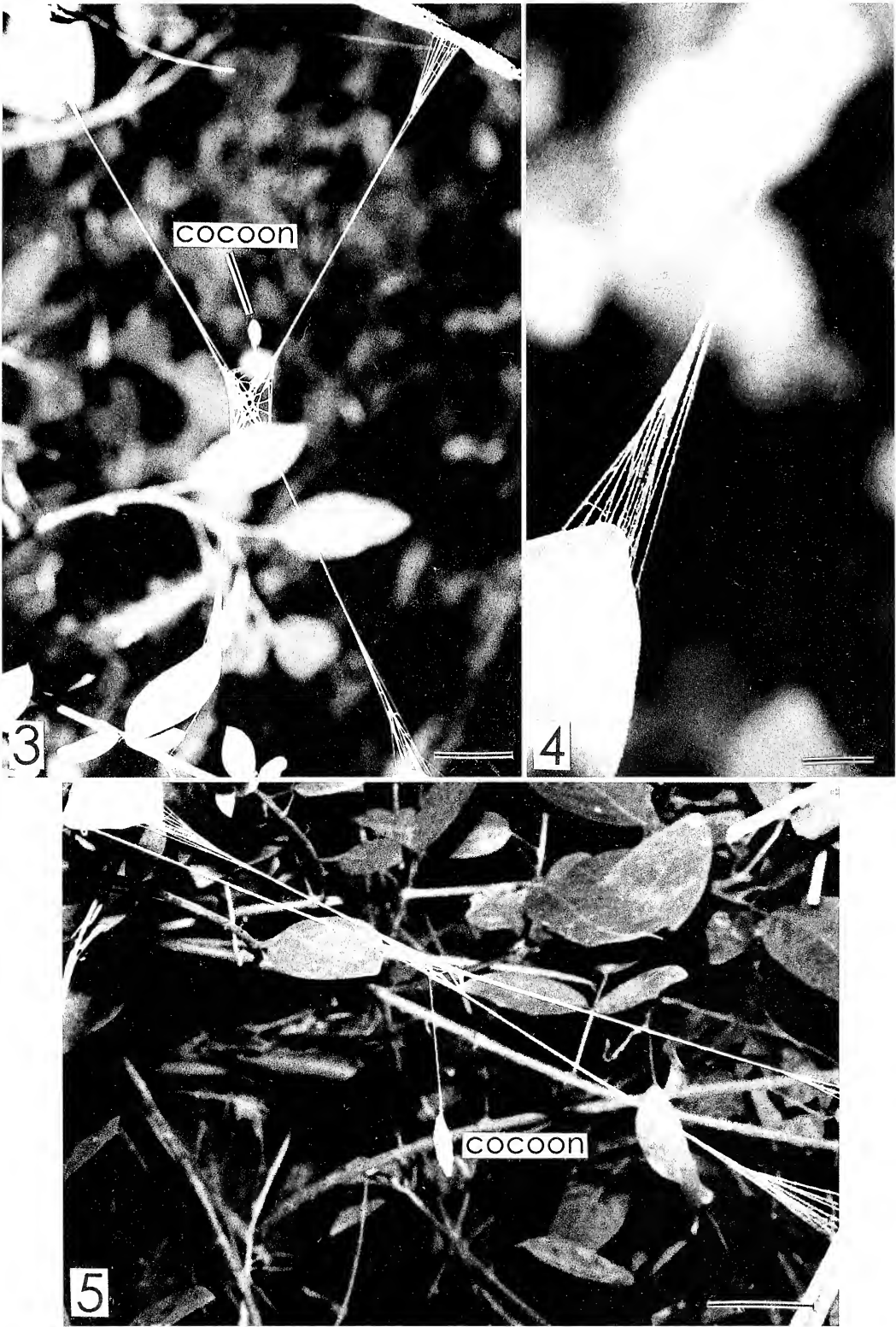
Figures 3–5.—Typical cocoon web. 3. Dorsal view. Scale bar = 3.0 cm; 4. Detail of attachments to a leaf. Scale bar = 0.5 cm; 5. Lateral view. Scale bar = 3.0 cm.

dial lines had many branches near their tips and were thus attached at many adjacent points to the substrate (Fig. 4). They were also sometimes attached at multiple points in the central area. There were several other indications, in addition to the planar arrangement of radial lines, that the webs from which cocoons were suspended represented modified orbs. Some cocoon webs had circular lines similar to those at the hubs of normal orbs (17% of 41 webs checked for this detail) (Figs. 6, 7), though in no case was the central portion of the hub empty, as in normal orbs. Some had one or more frame lines connecting the radial lines (29% of 42 webs checked for this detail) (Fig. 6). These frames were typically much shorter and nearer the hub than were the frame lines of normal orbs (Fig. 1). The most elaborate cocoon web had a distinct hub, frame lines, and a mesh above and below the hub. At the opposite extreme, the two simplest cocoon webs consisted of a single strong line with the larva or the cocoon hanging from the central portion.

Cocoon webs spanned smaller spaces than normal orbs of mature females. The distance between the two most distant points of attachment of anchor lines was smaller in cocoon webs (mean 36.6 ± 17.2 cm in a sample of 38) than in orbs (99.6 ± 47.5 cm in a sample of 31) ($P < 0.001$ with Mann Whitney U-Test). These cocoon webs also had fewer anchor lines (lines directed to the substrate) (mean 3.9 ± 1.5 for cocoon webs, 5.3 ± 1.7 for the orbs; $P < 0.001$ with Mann-Whitney U-Test).

Construction behavior.—Cocoon web construction behavior, observed in five spiders captured in the field the same day with larvae and a sixth three days after being collected, was very consistent. Early in the evening, the spider built several lines, repeatedly removing and shifting the points of attachment as typically occurs during the preliminaries of orb construction of many species of orb weavers (Tilquin 1942; Eberhard 1990). It then remained more or less immobile until between 23:30 and 01:00, when construction activity occurred in bursts. Typically the spider added one to several radial lines in quick succession, and then spent a minute or more (up to 30 min) immobile at the hub before the next burst of activity. The spider's movements showed no signs of weakness or vacillation, and it

moved directly from one attachment to the next as in normal frame and radius construction.

Radial lines were all in nearly the same plane and were added to the web using two similar, simple behavior patterns (Fig. 8, A and B). The spider began by attaching its dragline at the hub, then walked toward the substrate along a radial line, walked along the substrate a short distance and attached the line it had laid from the hub (A_1, B_1). Then it returned to the hub, laying a second dragline as it walked along this line or another radial line that it had laid previously and attached it at the hub (A_2, B_2). When the substrate was thin (a strand of wire, for instance) the spider usually moved to the opposite side to make the attachment before returning to the hub, as is typical of frame construction in orbs (Tilquin 1942; Eberhard 1990).

The two patterns differed in that either the lines were laid without attachments to previously laid radial lines (A_1, A_2 in Fig. 8), or (more often) the spider attached its dragline one or more times to radial lines both on the way out and on the way back to the hub (B_1, B_2 in Fig. 8). Consecutive radial lines were always laid in different directions, as in orb construction by other araneoid spiders (Tilquin 1942; Dugdale 1969; Le Guelte 1966; Witt et al. 1968; Eberhard 1982). Each radial line was reinforced repeatedly, and the total amount of dragline silk in a cocoon web probably represented a major fraction of that in an orb. The estimated total numbers of radial lines in two finished cocoon webs were 36 and 30. Thus the number of radial trips was on the same order as the typical number of radii (20–35) in a normal orb (Fig. 1).

The behavior of one further individual, collected four days previously and observed in San Antonio de Escazu, was very different. The spider descended to the floor about 1.5 below the wire hoop, formed a "hub" where several lines converged about 1 cm above the floor, and then made 5–10 very long radial excursions (up to 1.3 m each) walking on the surface of the floor. As it moved away from the hub it walked in a nearly straight line, attaching its drag line periodically to the floor, but in some cases it gradually made an arc of up to more than 180° before it turned back and slowly retraced its path back to the hub. On at least four occasions the spider encoun-
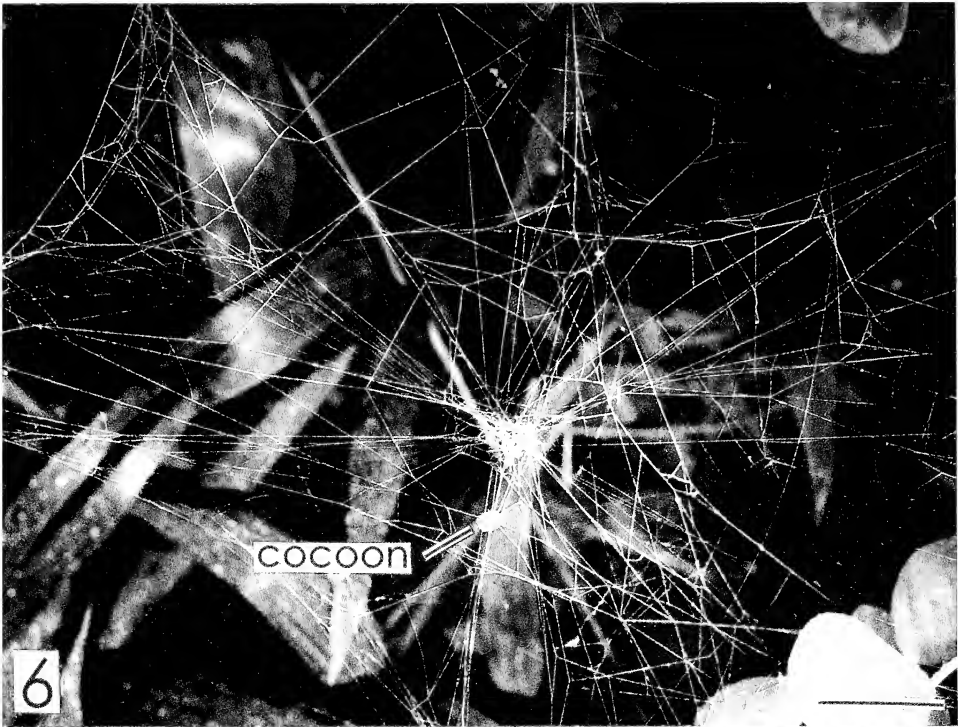
Figures 6–7.—Dorsal view of an unusually elaborate cocoon web with hub loops and a frame line. Scale bars = 2.5 and 1.0 cm respectively.
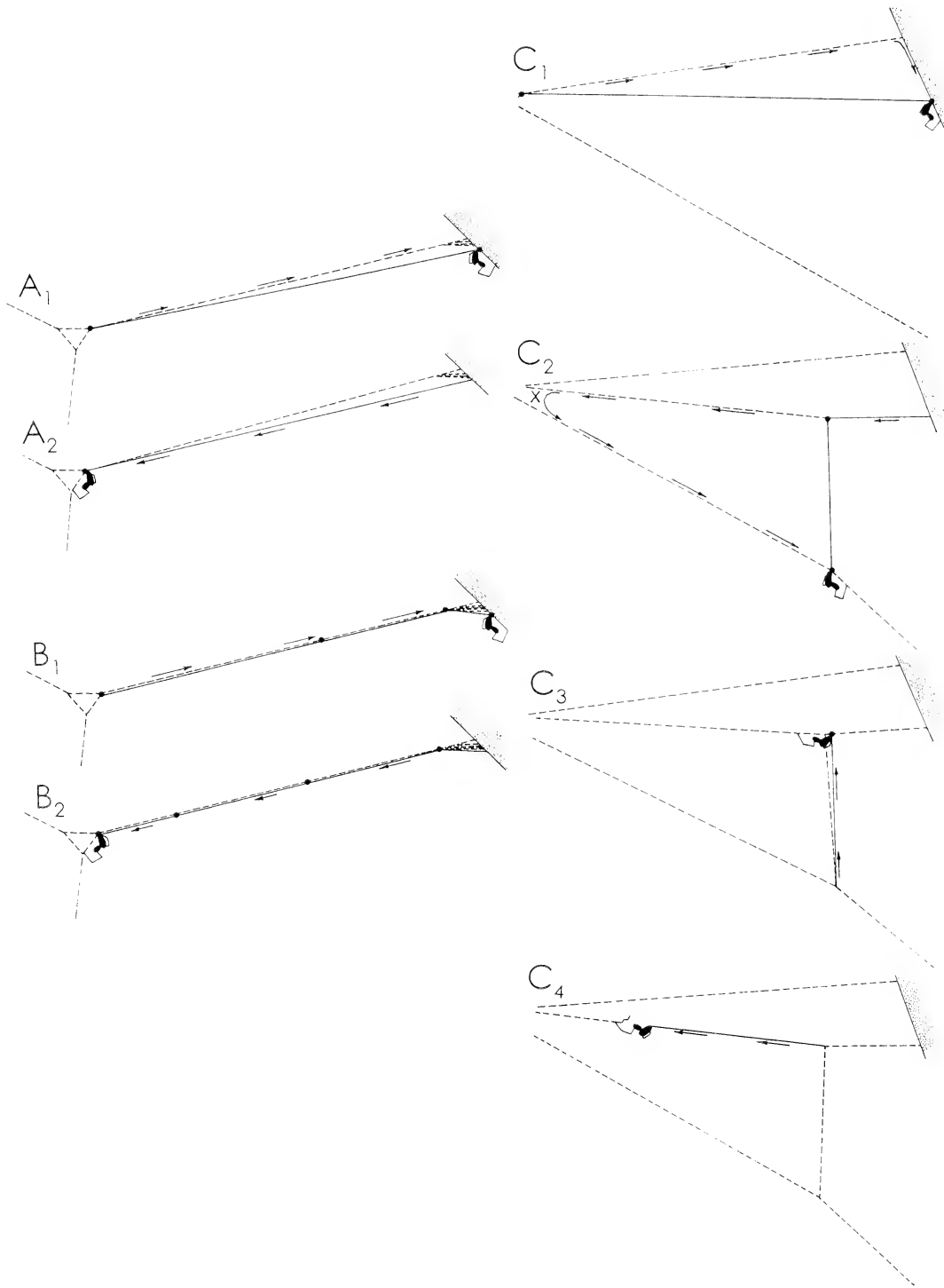
Figure 8.—Diagrammatic representations of the sequences of behavior during construction of a cocoon web (A_1–A_2, and B_1–B_2) and a frame line in a typical orb (C_1–C_4). Stippling represents substrate, black spots represent points where the dragline was attached, and dashed lines represent lines laid earlier in the sequence (C_1–C_4 after Eberhard 1990). Cocoon web construction corresponds to the behavior in C_1 and the first part of C_2.
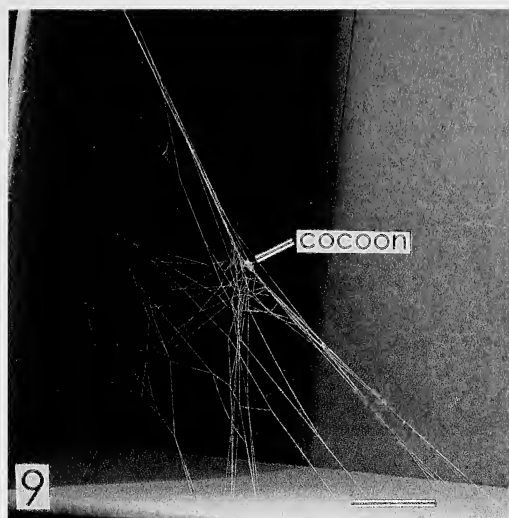
Figure 9.—Dorsal view of a web made by a mature male on the night that it was killed by a wasp larva. Note multiple attachments to substrate of some radial lines (as in Figs. 4 and 10). Scale bar = 3.0 cm.

tered an object that it could have climbed and thus have raised its drag line off the floor, but instead it struggled on across the floor. When I then removed the larva, and replaced the spider on the wire hoop after breaking the lines leading downward toward the floor, the spider again descended to the floor where it made another hub.

Wasps generally avoided parasitizing mature males (Eberhard 2000), but two larvae on mature males matured and made cocoons in captivity. One male spider did not make a cocoon web (or indeed any supporting structure whatsoever); the wasp's cocoon hung from a single short strand of spider silk. The second parasitized mature male spider, however, built an extensive web that resembled a cocoon web in being more or less planar, and having many attachments to the substrate on the night that it was killed and consumed by the larva (Fig. 9).

Experimental removal of larvae.—Larvae were removed from 22 spiders in captivity on the evening when the spider was to be killed. Four spiders built no webs that night. The 18 webs that were built were of three types. Three were more or less typical cocoon webs, with a low number of radial lines which were composed of multiple strands that were attached at many adjacent points on the sub-

strate, and more or less converged at the hub (Figs. 10, 11). A fourth spider, which had already begun cocoon web construction when I removed the larva, resumed cocoon web construction but did not return consistently to the hub, and made two additional "hubs". Simplified, "vestigial" webs, that had only a few more or less radial lines converging at the point where the spider rested and large masses of silk lines loosely packed together near the central area, were built by 13 spiders (Figs. 12, 13). These radial lines were attached to the substrate at only one or at most a few points. Vestigial webs never had hub loops, temporary spirals or sticky lines, and only seldom had recognizable frame lines. One further web was a nearly normal orb, except that the center of the hub was not removed and some portions of the sticky spiral lacked sticky balls.

The construction behavior of spiders from which larvae had been removed was observed for two cocoon webs and three vestigial webs. Cocoon web construction was very similar to that described above for spiders carrying larvae, including the frequent pauses between bursts of construction behavior, except that on some occasions the spider failed to attach its drag line at the hub when it returned after laying a radial line. The drag line laid on the next trip away from the hub was thus not attached at the hub, but originated part way out the previous radial line (line 2–4 in B_2 of Fig. 14). When this behavior was repeated over and over, the hub gradually expanded and became dispersed. The resulting web had large numbers of more or less radial lines attached to the substrate close to each other, but a diffuse central area (Fig. 15).

During vestigial web construction, the spider also made radial lines attached to the substrate just as above. On some return trips to the hub area, however, it broke and removed these lines, reeling them up and leaving them packed loosely together attached to the web. The final product of this process of repeatedly laying and then removing lines was a scanty array of more or less radial lines, and one or more large masses of fluff (Fig. 13).

None of the 22 experimental spiders that built webs died on the evening the wasp larva was removed. In nine cases the spider built a second web on the following night, and the second web was of the same type built on the
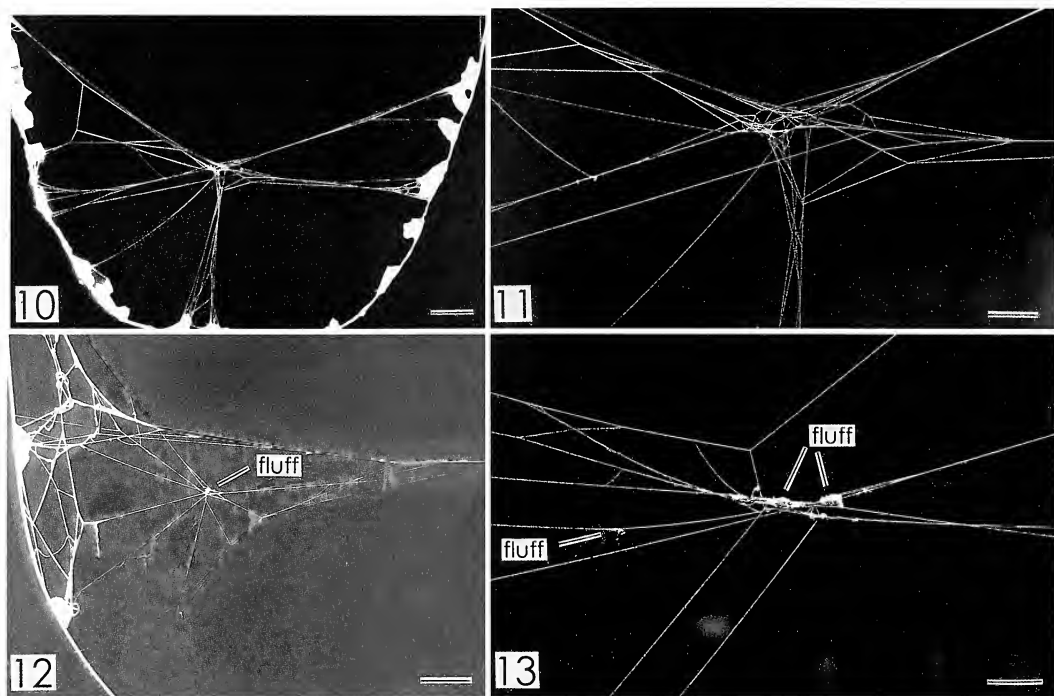
Figures 10–13.—Webs made by spiders from which the wasp larva was removed on the night when the larva would have normally killed the spider. 10. Cocoon-web type, in which the few radial lines each had multiple attachments to the substrate. Scale bar = 3.0 cm. 11. Close-up of hub of web in Fig. 10. Scale bar = 1.0 cm. 12. "Vestigial" type web, in which a few radial lines were attached singly to the substrate (heavy white lines are from previous web of another spider). Scale bar = 3.0 cm. 13. Close-up of the hub of a vestigial web (different web from that in Fig. 12), showing several masses of fluff. Scale bar = 1.0 cm; all wire hoops were horizontal.

first (two cocoon webs, seven vestigial webs). Five of the second vestigial webs had at least one hub loop. Due to deaths and emigrations, it was not possible to follow the spiders' behavior systematically on subsequent nights. Two spiders survived for a week, and gradually built webs that were progressively more orb-like though still substantially altered (Fig. 16).

DISCUSSION

Comparison of cocoon web construction behavior with the early stages of normal orb construction (Eberhard 1990) indicates that it is probably homologous with the early steps of type "D" frame construction (Fig. 8 C_1–C_4). Most anchor line construction in an orb involves removal of lines already in place, or shifting their attachments to each other (Tilquin 1942; Eberhard 1990), but neither of these behavior patterns was ever seen during cocoon web construction. In type D anchor construction, however, which sometimes occurs as part of frame construction, the early stages do not involve removing or shifting lines (Fig. 8 C_1, C_2). Premature termination of this type of frame construction behavior when the spider returns to the hub after the first attachment to the substrate and followed by attachment of the spider's drag line at the central area (x in Fig. 8 C_2), would result in a sequence of operations identical to type A cocoon web construction (Fig. 8 A). Adding attachments to the line already in place on the way out would result in a sequence similar or identical to the second type of cocoon web construction behavior (Fig. 8 B). Similar attachments sometimes occur in the closely related *L. mariana* during frame construction of types "A" and "C" of Eberhard (1990) but were not seen in conjunction with type D of Eberhard (1990) (the same individual often performed more than one type while building a given orb). A further resemblance to attach-

Figure 15.—Cocoon-type web with dispersed hub built by a spider from which the larva was removed on the evening on which it would have normally killed its host. Scale bar = 3.0 cm; wire hoop was horizontal.

Figure 16.—Orb-like web built by a partially recovered spider. The wasp larva had been removed five days earlier, on the evening when it would have killed the spider, and the spider had spun a typical vestigial web on that night. Scale bar = 2.0 cm.

Figure 14.—Diagrammatic representations of cocoon web construction behavior of a spider with a wasp larva (A_1, A_2) and a spider from which the wasp larva had been experimentally removed (B_1, B_2). The experimental spider sometimes omitted the final attachment at the hub typical of cocoon web construction (attachment 3 in A_1 and A_2; see also Fig. 8 A_2 and B_2); when it moved away from the hub to make the next radial line, the dragline was thus displaced away from the hub (line 2–4 in B_2). Repeated omissions of this attachment resulted in a diffuse central area of the web (Fig. 15).

ments of anchor lines built during orb web construction by other orb weavers (Tilquin 1942: Eberhard 1990) was the attachment of radial lines to thin objects by moving to the opposite side of the object just before attaching. Thus, the spider built the cocoon web by apparently repeating the first portions of one type of frame construction over and over. Fur-

ther evidence that cocoon webs were homologous with orbs is the fact that when these webs had more than three radial lines, these were nearly always in approximately the same plane. In addition, some cocoon webs had frame lines, and a few had hub loops (Figs. 6, 7).

The homology of cocoon and orb webs emphasizes that perhaps the most extraordinary aspect of the wasp larva's effect on the spider was not so much what the spider did, but what it did not do. Many aspects of normal orb con-

struction were completely absent, including both breaking, reeling up and replacing lines (e.g. Fig. 8 C$_4$), and breaking and then re-attaching lines. These two behavior patterns form integral parts of most types of both frame and radius construction in normal orbs of this and other species (Tilquin 1942; Eberhard 1982 1990; Coddington 1986). A single failure to repress these behavior patterns could be disastrous for the wasp larva, as it would result in the removal of the many-stranded cable of radial lines, and its replacement with a much weaker line. This indeed occurred in the vestigial webs built by spiders from which larvae were experimentally removed. Also completely missing were production of the temporary spiral and sticky spiral, and removal of the central portion of the hub at the end of orb construction, which again would have resulted in considerable weakening of the support for the wasp's cocoon. These differences between cocoon webs and normal orbs are appropriate to make the cocoon web stronger and less likely to be damaged by falling debris, and thus a more durable support for the wasp's cocoon than an orb would be. Strong support for the cocoon may be important for the wasp's survival, as in the related *Hymenoepimecis robertsae* some pupae died when heavy rains damaged cocoons (Fincke et al. 1990).

The importance of the precision of the behavior induced in the spider is also illustrated by the effect of occasional omission of one normal detail, the final attachment at the hub after a radial line was built (Fig. 8 A$_2$, B$_2$) that was seen in some spiders from which the larvae were experimentally removed. The resulting lack of a clear central point of convergence produced webs that were much less appropriately designed to support the wasp's cocoon (Fig. 15). It is not clear whether the aberrant behavior of one spider that laid radial lines on the surface of the floor instead of in the air was something that happens in nature (such webs would be missed in the field) or was an artifact of captivity.

In some cases, claims that modification of host behavior associated with parasitism represents an evolved adaptation by the parasite to promote its own reproduction have been controversial (Toft et al. 1991; Poulin 2000). There can be little doubt on this score with the species of this study, as the cocoon web

design is both unprecedented in *P. argyra* or any closely related orb weaver, and seems especially appropriately designed to increase the survival of the wasp. Induction of spinning behavior also occurs in several families of spiders parasitized by acrocerid flies; the spider spins a thin cell similar to that made just prior to moulting, and the larva clings to the web after emerging from the spider (Schlinger 1952, 1960, 1987).

The changes in the behavior of *P. argyra* are induced chemically rather than by direct physical interference with the spider's nervous system. The wasp larva contacts only the surface of the spider's abdomen and limits itself to making small holes through which it imbibes hemolymph (Eberhard 2000a,b). In addition, some spiders built normal cocoon webs after the larva was removed. Some ichneumonids modify host behavior and physiology via products injected by the female wasp when she oviposits (Gauld 1995). However, the lack of web modification in the days immediately following the attack by the wasp, the sudden abrupt shift in behavior that is coordinated with maturation of the larva, and the changes in webs produced by removing the larvae, all argue that the larva rather than the adult female wasp induced modified web construction behavior. Secretion of neuromodulators by parasitoid larvae has been implicated in behavioral changes produced in some insect hosts (Beckage 1997). The variety of web forms and construction behavior observed when the larva was removed prematurely suggest a complex, gradual effect rather than an abrupt, simple modification.

The ability of *Hymenoepimecis argyraphaga* to induce specific behavior patterns in spiders indicates that even these fine behavioral details are independent units or modules at some level within the spider, and not just artificial constructs. The additional web forms produced by experimentally removing larvae from spiders suggest even further subdivisions of building behavior. The problem of what constitutes a biologically realistic behavioral unit is crucial in the use of behavior patterns as taxonomic characters in orb-weavers Eberhard 1982; Coddington 1986, 1990; Scharff & Coddington 1997; Griswold et al. 1998) as well as in other animals (Wenzel 1992). The results of this study suggest that it is reasonable to attempt to use even finer behavioral

details than those that have been used previously in orb weaver taxonomy. The cocoon web of *P. argyra* is similar to the secondarily reduced "asterisk" web found by Stowe (1978) in the distantly related araneid *Wixia ectypa* (Walckenaer). Whether or not this evolutionary transition involved chemical changes similar to those produced by *H. argyraphaga* remains to be determined.

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LITERATURE CITED

Barnard, C.J. & J.M. Behnke. 1990. Parasitism and Host Behaviour. Taylor & Francis, London.

Beckage, N.E. 1997. New insights: how parasites and pathogens alter the endocrine physiology and development of insect hosts. Pp. 3–36. *In* Parasites and Pathogens, Effects on Host Hormones and Behavior (N.E. Beckage, ed). Chapman and Hall, New York, New York.

Coddington, J.A. 1986. Monophyletic origin of orb webs. Pp. 319–363, *In* Spiders, Webs, Behavior and Evolution (W. Shear, ed). Stanford University Press.

Coddington, J.A. 1990. Cladistics and spider classification: araneomorph phylogeny and the monophyly of orbweavers (Araneae: Araneomorphae; Orbiculariae). Acta Zoologica Fennica 190:75–87.

Dugdale, B.E. 1969. The weaving of an engineering masterpiece, a spider's orb, done at Fryson Lakes, N. J., August 8, 1942, as observed and reported by B. E. Dugdale, structural engineer. Natural History 78(3):36–41.

Eberhard, W.G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. Evolution 36:1067–1095.

Eberhard, W.G. 1988. Behavioral flexibility in orb web construction: effects of silk supply in different glands. Journal of Arachnology 16:303–320.

Eberhard, W.G. 1990. Early stages of orb construction by *Philoponella vicina, Leucauge mariana,* and *Nephila clavipes* (Araneae: Uloboridae and Tetragnathidae), and their phylogenetic implications. Journal of Arachnology 18:205–234.

Eberhard, W.G. 2000a. Manipulation of host spider web construction behavior by a wasp larva. Nature 406:255–256.

Eberhard, W.G. 2000b. The natural history and behavior of a parasitoid, *Hymenoepimecis argyra-phaga* (Hymenoptera, Ichneumonidae) and its host, the spider *Plesiometa argyra* (Araneae, Tetragnathidae). Journal of Hymenoptera Research 9:220–240.

Eberhard, W.G., S. Guzman-Gomez & K.M. Catley. 1993. Correlation between spermathecal morphology and mating systems in spiders. Biological Journal of the Linnean Society 50:197–209.

Fincke, O., L. Higgins & E. Rojas. 1990. Parasitism of *Nephila clavipes* (Araneae, Tetragnathidae) by an ichneumonid (Hymenoptera, Polysphinctini) in Panama. Journal of Arachnology 18:321–329.

Gauld, I.D. 2000. The re-definition of pimpline genus *Hymenoepimecis* (Hymenoptera: Ichneumonidae) with a description of putatively plesiomorphic new Costa Rican species. Journal of Hymenoptera Research 9:213–219.

Gauld, I.E., J. Ugalde & P.E. Hanson. 1998. Guia de los Pimplinae de Costa Rica. Revista de Biologia Tropical. 46 (Supl. 1):1–189.

Godfray, H.C. J. 1994. Parasitoids Behavioral and Evolutionary Ecology (Princeton University Press, Princeton, New Jersey.

Griswold, C. E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zoological Journal of the Linnean Society 123:1–99.

Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web construction behavior in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae, Tetragnathidae). Australian Journal of Zoology 43:313–364.

Ibarra, G., O. Jaramillo M. & T. de Castro C. 1991. Observaciones sobre el comportamiento reproductor de las arañas del género *Leucauge* (Araneae: Tetragnathidae) del Soconusco, Chiapas, Mexico. Pp 65–66. Memorias del 26 Congreso Nacional de Entomologia, Veracruz, Mexico.

Jenni, L., D.H. Molyneux, J.L. Livesley & R. Galun. 1980. Feeding behaviour of tsetse flies infected with salivarian trypanosomes. Nature 283: 383–385.

Le Guelte, L. 1966. Structure de la toile de *Zygiella x-notata* Cl. (Araignées, Argiopidae) et facteurs qui régissent le comportemente de l'araignée pendant la construction de la toile. Thése Publications de l'Universite Nancy Faculte des Sciences.

McLachlan, A. 1999. Parasites promote mating success: the case of a midge and a mite. Animal Behaviour 57:1199–1205.

Poulin, R. 1994. Meta-analysis of parasite-induced behavioural changes. Animal Behaviour 48:137–146.

Poulin, R. 2000. Manipulation of host behaviour by parasites: a weakening paradigm? Proceedings of the Royal Society of London, Series B 267:787–792.

Scharff, N. & J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zoological Journal of the Linnean Society 120:355–434.

Schlinger, E.I. 1952. The emergence, feeding habits, and host of *Opsebius diligens* Osten Sacken. Pan-Pacific Entomology 28:7–12.

Schlinger, E.I. 1960. A revision of the genus *Ogcodes* Latrielle with particular reference to species of the Western Hemisphere. Proceedings of the United States National Museum 111:227–336.

Schlinger, E.I. 1987. The biology of Acroceridae (Diptera): true endoparasitoids of spiders. Pp. 319–327, *In* Ecophysiology of Spiders (W. Nentwig, ed.). Springer-Verlag, New York.

Stowe, M.K. 1978. Observations of two nocturnal orbweavers that build specialized webs: *Scoloderus cordatus* and *Wixia ectypa* (Araneae: Araneidae). Journal of Arachnology 6:141–146.

Tilquin, A. 1942. La Toile Géometrique des Araignées. Presses Univ. France, Paris.

Toft, C.A., A. Aeschlimann & L. Bolis. 1991. Parasite–Host Associations. Oxford University Press, New York.

Wenzel, J.W. 1992. Behavioral homology and phylogeny. Annual Review of Ecology and Systematics 22:361–381.

Wickler, W. 1976. Evolution-oriented ethology, kin selection, and altruistic parasites. Zeitschrift für Tierpsychologie 42:200–214.

Witt, P.N., C. Reed & D.B. Peakall. 1968. A Spider's Web Springer, New York.

LIFE-CYCLES OF FOUR SPECIES OF *PARDOSA* (ARANEAE, LYCOSIDAE) FROM THE ISLAND OF NEWFOUNDLAND, CANADA

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ABSTRACT. Populations of four species of *Pardosa, P. fuscula, P. groenlandica, P. hyperborea* and *P. moesta,* were sampled during summer 1997 on the west coast of the Island of Newfoundland, Canada. Measurements of carapace width indicated that all four species fit a biennial life-cycle model where new individuals join the population in summer, live through the following winter, grow throughout the next year, live through the next winter, and then mature, breed and die in the year following their second winter. All species showed only one defined recruitment of new spiderlings during the sampling period, but at least two species may have extended periods of recruitment and some individuals may have an extended life-cycle.

Keywords: Lycosidae, *Pardosa,* life-cycle

At the beginning of the 20th century the conventional wisdom about araneomorph spider life-cycles was that most were annuals, either spring breeders or summer-autumn breeders (Emerton 1902). Palmgren (1939) provided one of the first exceptions when he described the two-year cycle of *Dolomedes fimbriatus* (Clerck 1757) where juveniles overwintered twice. Cloudsley-Thompson (1955) concluded that individuals of all three British species of *Amaurobius* C. L. Koch 1837 lived for about two years, overwintered twice, and spent their second winter as adults. Hackman (1957) described a similar two-year cycle for *Trochosa ruricola* (De Geer 1778). Dondale's (1961) seminal work presented quantitative data for five species of spiders in Nova Scotia, Canada: *Araniella displicata* (Hentz 1847), *Philodromus rufus* Walckenaer 1826, *P. cespitum* (Walckenaer 1802) and *Eris militaris* (Hentz 1845) were shown to be true biennials, while *Pelegrina proterva* (Walckenaer 1837) was annual. He also concluded that nine other widespread and abundant spiders were biennials. In the last decades of the 20th century a number of studies have not only clearly demonstrated annual and biennial life histories for several different species, but also reported permutations of these two basic life-cycles. That is, within these two general categories there are species that mature and breed at different times of year and species that are

intermediates between strictly annual and strictly biennial (e.g. Eason & Whitcomb 1965; Toft 1976, 1979; Dondale 1977; Stratton & Lowrie 1984).

In addition to such permutations of the annual/biennial theme, the plasticity of spider life history has been demonstrated. For example, the same species may change from annual to biennial depending on geographical location, such as *Philodromus cespitum* that was annual on the warmer Niagara Peninsula, Ontario, Canada (Putman 1967), but biennial in colder Nova Scotia, Canada (Dondale 1961). *Pardosa lugubris* (Walckenaer 1802) was annual in the Netherlands (Vlijm et al. 1963) but biennial in Scotland, and this was attributed to differences in summer temperatures (Edgar 1971a, 1972). In addition, individuals of the same population may extend their life-cycle under particular circumstances. Edgar (1972) showed that *P. lugubris* in the Netherlands varied between annual and biennial depending on environmental conditions. Workman (1978) showed that in Norfolk, U.K., *Trochosa terricola* Thorell 1856, usually biennial with the second overwintering as adults, was occasionally triennial when juveniles hatched from late or second cocoons overwintered three times before breeding in their fourth year. Leech (1966) suggested that even more extended life-cycles may occur in particularly cold conditions. He surmised that two species

from Hazen (Ellesmere Island, NWT, Canada), *Pardosa glacialis* (Thorell 1872) and *Alopecosa exasperans* (O. Pickard-Cambridge 1877), had a life-span of six or seven years, but that surmise was based on the unsupported assumption that each of the estimated six or seven instars lasted one year. These points raise a number of questions. Do spider species not yet examined have similar life histories to those already described? Do species in places not yet examined have similar life histories to those in known places? Do species at latitudes farther north than some of those previously examined show extended life histories, for example intermediate between those documented in Nova Scotia (Dondale 1961) and those hypothesised on Ellesmere Island (Leech 1966)?

The Island of Newfoundland is an appropriate location to examine these questions. The life histories of the species in this study have not been described before with the following exceptions. Ricards (1967) reported the life history of what he called *P. groenlandica* (Thorell 1872) in Montana, and Schmoller (1970) reported on what he called *P. tristis* Keyserling 1887 (identified as *P. groenlandica* by Dondale 1999) in Colorado. But as Dondale (1999) pointed out, both authors were in fact dealing with complexes of two or more species, not monospecific populations of *P. groenlandica,* so their conclusions have limited significance. Buddle (2000) reported the life-cycle of *Pardosa moesta* Banks 1892 in Alberta, and his observations are directly relevant here. Life histories of spiders on the Island of Newfoundland have essentially never been investigated. Hackman (1954) reported 220 species from the Island, but drew conclusions for only one: *Trochosa terricola* was described as biennial, although the data presented could support other interpretations.

The present study sites on the Island of Newfoundland, at approximately 50°N, are farther north than previous life history work with the following exceptions. Buddle (2000) and Zimmerman & Spence (1998) reported life-cycles of lycosids and a pisaurid, respectively, from approximately 54°N in central Alberta. However, both these studies were conducted at the George Lake area dominated by hardwoods such as aspen (indicative of higher summer temperatures) in the boreal transition region, whereas the present study was conducted in boreal forest dominated by fir and spruce (indicative of lower summer temperatures) (Ecological Stratification Working Group 1995). Leech (1966) reported from the Canadian arctic at approximately 82°N. Some European work has been conducted at latitudes farther north than Insular Newfoundland. For example, Toft (1976) reported from Denmark and Edgar (1971a) from Scotland, both at approximately 56°N. However, climate is not simply determined by latitude, and the generally more temperate European climate is indicated by the beech woods of the former study and the oak woods of the latter.

METHODS

Species and localities.—Four species of *Pardosa* C. L. Koch 1847 (Lycosidae) were chosen for this study: *P. fuscula* (Thorell 1875), *P. groenlandica, P. hyperborea* (Thorell 1872) and *P. moesta.* Full descriptions of these species can be found in Dondale & Redner (1990). They were chosen both because the taxonomy of most Canadian lycosids is well established (Dondale & Redner 1990) so conclusions could be confidently assigned to individual species and preliminary investigations in 1995 and 1996 found dense populations of these species. Such dense populations lend themselves to sampling by hand as opposed to using pitfall traps. Pitfall traps are useful measures of activity and have a long history of employment in ecological studies, but they are selective in trapping different species and different life-stages (Berghe 1992; Topping & Sunderland 1992).

The Island of Newfoundland is in the boreal shield ecozone where the climate is heavily influenced by arctic currents, many areas are exposed to particularly harsh climatic conditions and the landscape is dominated by spruce-fir forest with extensive peatlands. Within that ecozone, the populations of this study were in, or immediately adjacent to, the northern peninsula ecoregion (South 1983; Ecological Stratification Working Group 1995).

The populations chosen were all in Gros Morne National Park, Newfoundland, and were therefore largely protected from human interference. The *P. fuscula* population was on an extensive peatland immediately below and around the highest land on top of Partridgeberry Hill behind the community of Woody

Point (49°30.2'N, 57°56.9'W). The *P. groenlandica* population was at the back of a pebble-cobble beach immediately north of the mouth of Baker's Brook (49°39.5'N, 57°57.7'W). The *P. hyperborea* population was on the extensive treeless heath on the higher parts of Partridgeberry Hill behind Woody Point (49°30.0'N, 57°56.6'W). The *P. moesta* population was on the treeless coastal meadow immediately above and behind the beach at Lower Head, Shallow Bay (49°57.3'N, 57°46.2'W). Voucher specimens are deposited in the Newfoundland Museum (catalogue numbers NFM ARA-01, -02, -03 and -04).

Measurements.—Dondale (1961) concluded that carapace width (CW) was the most generally useful measurement to distinguish life history stages but the species he examined did not include lycosids. Hagstrum (1971) confirmed the essentials of that work with measurements of the lycosid *Alopecosa kochi* (Keyserling 1877). However, Toft (1976) claimed that linear measurement of tibia I gave the best discrimination between instars, but in support presented data for only one species, the linyphiid *Helophora insignis* (Blackwall 1841). His data supported the superiority of tibia I measurements for that particular species, but what is applicable to a linyphyiid may not be applicable to lycosids. To resolve this question, CW and tibia I of a number of samples of the lycosids of the present study were compared.

Life-cycles.—Critical information for all four species was whether adults survived the winter and the general nature of the population immediately after the winter. Samples were therefore taken just after snow-melt at each site (May or early June). Preliminary observations in 1995 and 1996 indicated that no adults were seen until July, except adult *P. groenlandica* which appeared in June. Therefore in 1997, sampling of *P. groenlandica* commenced in May and of the other species in June. At each sampling I tried to catch at least 50 specimens. I achieved this in all but the June samples of *P. groenlandica* and *P. fuscula,* when bad weather made these two larger and less numerous species harder to find. In one instance, *P. groenlandica* in June, it was necessary to sample the population on two consecutive days, June 1 and 2. Sampling dates and numbers caught for each species in 1997 are as follows. *P. moesta*: June 2, 98;

July 7, 99; August 14, 143; September 14, 88. *P. hyperborea*: June 5, 74; July 3, 75; August 11, 55; September 15, 66. *P. fuscula*: June 5, 48; July 9, 135; August 11, 54; September 15, 104. *P. groenlandica*: May 15, 60; June 1 and 2 combined, 37; July 4, 68; August 12, 62; September 13, 74. Spiders were caught with an aspirator and transferred to snap-cap plastic vials. Only one spider was put in each vial to avoid intraspecific aggression and cannibalism. Spiders were taken to the laboratory, placed in a deep-freeze until comatose and then placed directly into 75% ethanol for storage and later examination.

Although considered superior to pitfall traps for present purposes, hand collection nevertheless has two principal imperfections: lycosids are weather-sensitive (Vlijm & Kessler-Geschiere 1967) and may not be visible except under warm and windless conditions, and data from hand collections can be misleading because of conscious or unconscious size-selection by the collector. To offset weather problems, collections were made as far as possible on favorable days, when at least two individuals of the selected species were visible in a five-minute preliminary inspection. To offset size-selection, a conscious effort was made to catch all individuals seen of the target species irrespective of size.

Life-stages identified.—Three separate life-stages were identified: immature, subadult and mature. Mature contains a single instar and is clearly defined as adult males with fully developed functional palps and adult females with fully developed functional epigyna. The boundary between mature and subadult is clear cut. Subadults are close to becoming mature, presumably within a molt or two of maturity (although total number of molts and number of molts within the subadult stage are unknown). Secondary sexual characters are pronounced but not complete: male palpal tarsi are significantly swollen with ventral surfaces showing pronounced ogee curves; developing female epigyna have obvious lateral sclerites. Immatures are either smaller specimens showing no differences that would indicate their future sex, or larger specimens with males showing at most a slight thickening of the palpal tarsi and females showing no development of the lateral epigynal sclerites and distinguishable from potential males only by virtue of having no sign of any palpal

Table 1.—Males and females (raw data) caught in 1997. (%) = females with cocoons.

	P. fuscula ♂, ♀	*P. groenlandica* ♂, ♀	*P. hyperborea* ♂, ♀	*P. moesta* ♂, ♀
June	0, 0 (0%)	2, 4 (0%)	0, 0 (0%)	0, 0 (0%)
July	19, 18 (89%)	2, 2 (50%)	21, 15 (47%)	35, 26 (4%)
Aug.	1, 6 (83%)	0, 5 (20%)	0, 24 (54%)	17, 50 (92%)
Sept.	0, 3 (0%)	0, 1 (100%)	0, 30 (80%)	0, 42 (43%)

swelling. The immature life-stage contains several instars. The boundary between immature and subadult is not always clear cut, and conclusions drawn from the data must be in light of this imprecision. In addition to these three stages, very small newly or recently hatched spiderlings will be referred to occasionally. These were easily identified because in previous years females of all four species carrying spiderlings had been caught and so the size range of new spiders was well known.

RESULTS

Measurements.—One example will illustrate the relative usefulness of measurements of the two different body parts. Figure 1 compares measurements of CW and tibia I length of the July 7 *P. moesta* sample and shows that both yield essentially similar information with the two different cohorts definitively separated and both larger and smaller cohorts spread over five or six units.

Life-cycles.—Numbers of individuals with different CWs for all four species populations are displayed in Figs. 2–5. Numbers of males and females caught and the percentage of those females carrying a cocoon are shown in Table 1. All four species fit the generalized life-cycle illustrated in Fig. 6. Adults appear around the end of June and the sexes are present in approximately equal proportions in July. Males then either vanish by August or decline rapidly in numbers and have gone by September. Based on the synchrony of the sexes, the mating season is principally late June and July. Females persist to at least mid September (when sampling stopped) but do not survive the winter. The breeding season (here defined as females carrying cocoons) is July through to September. New spiders hatch in mid to late summer and join a population consisting partly of mid-size immatures (hatched the previous year) and partly of ma-

tures that have just produced the new young. The two cohorts of immature individuals present at the end of the year survive the following winter and by the next spring have grown. The cohort of smaller immatures now becomes the mid-size cohort that will grow throughout the year. The cohort of larger immatures becomes sub-adult at or before the beginning of the year and then matures, breeds to produce a cohort of new spiderlings and in turn dies before the end of the year. In each species only one recruitment of new spiderlings was seen within the sampling period and there was no direct evidence that females make more than one cocoon. Individual species are considered below.

Pardosa moesta males and females appeared in July (Table 1). Males peaked in July, declined in August and were gone by September. That was similar to *P. fuscula,* whereas males of the other two species had gone by August. Breeding was slightly later than in the other species because only 4% of females carried cocoons in July and it was not until August and September that a significant percentage of females had cocoons. New spiderlings (modal CW 0.6 mm) appeared in September (Fig. 2), later than in *P. hyperborea* and *P.groenlandica* but the same time as *P. fuscula.* The apparent shrinkage of immatures between June and July is an artifact of sampling.

Pardosa hyperborea males and females appeared in July (Table 1), and males were seen only in July. Significant percentages of females carried cocoons in July, August and September. New spiderlings (modal CW 0.6 mm) appeared in August (Fig. 3). No new spiderlings were caught in September despite 80% of females carrying cocoons in that month. The group of immatures in September with modal CW of 1.0 mm is seen as the new spiderlings of August grown to that size. The similar group of small immatures in August
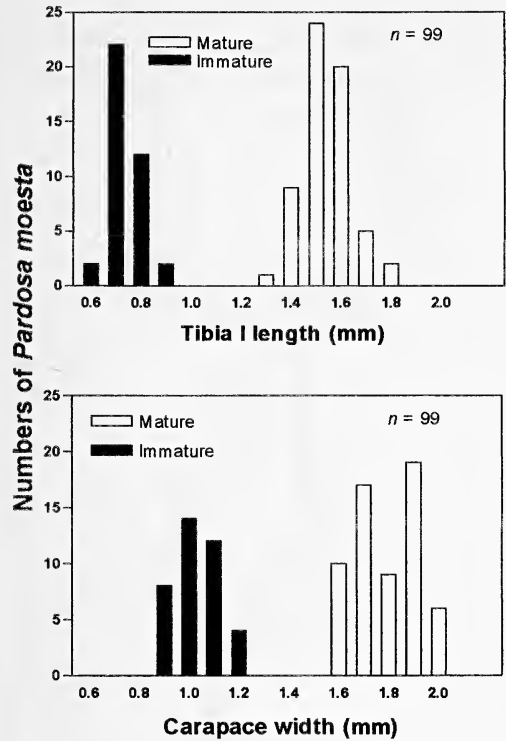
Figure 1.—Comparison of measurements of carapace width and tibia I length for the same sample of *Pardosa moesta* July 1997.

Figure 2.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa moesta*.

(CW 0.9–1.1 mm) is not seen as new spiders hatched the previous month (July) because neither adults nor cocoons were seen until July, and no new spiderlings were seen in that month. Therefore the two groups of immatures in August, lying between CW 0.9 and 1.6 mm, are seen as one group with a wide size range. That same group grew to occupy the range CW 1.1–1.8 mm in September. Therefore the breaks in the data at CW 1.2 mm in August and CW 1.6–1.7 mm in September are artifacts of sampling.

Pardosa fuscula males and females appeared in July (Table 1). Males had declined significantly by August and were gone by September. Breeding was in July and August with over 80% of females carrying cocoons in each of those months. New spiderlings (modal CW 0.6 mm) (Fig. 4) appeared in September.

Pardosa groenlandica males and females appeared in June (Table 1), the earliest appearance of adults in this study. Males were present in June and July but were gone by August. Females were still seen in September. Females carried cocoons in July and August,

and a single female with a cocoon was caught in September. New spiderlings (modal CW 0.8 mm) appeared in August (Fig. 5), and had grown to modal CW 1.0 mm by September. The single subadult taken in July (CW 3.4 mm) was the latest observation of this stage for any of the four species. Small numbers of small immatures (CW 0.8 mm) were also seen
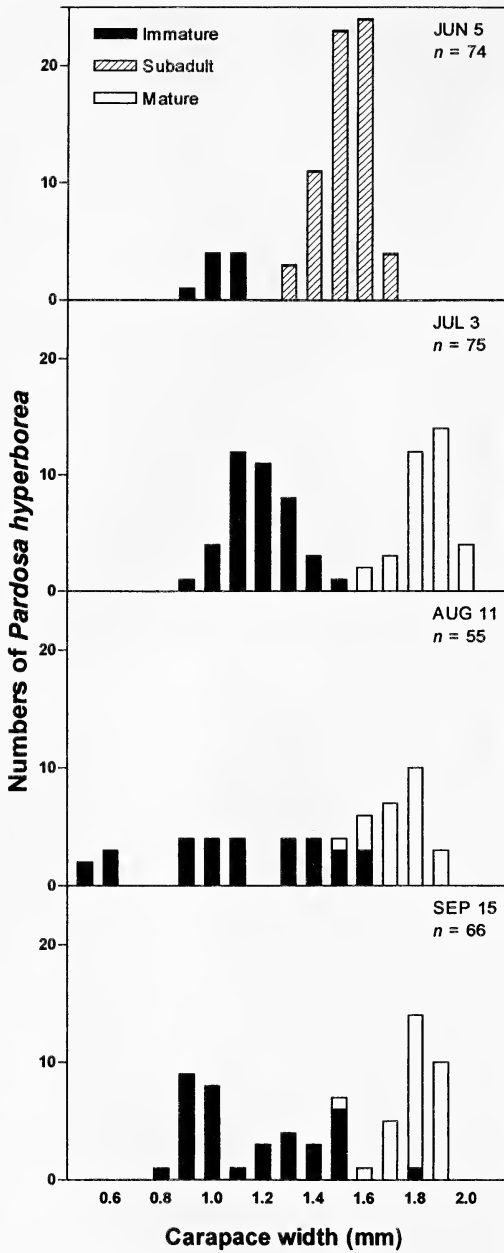
Figure 3.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa hyperborea*.

Figure 4.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa fuscula*.

in June and July. In July these might have been a small number of early-hatching new spiderlings because both sexes had been present the previous month, but the same explanation is not applicable to June because there was no evidence of cocoon production in that month. This is the only species of this study where subadults were seen in September. The
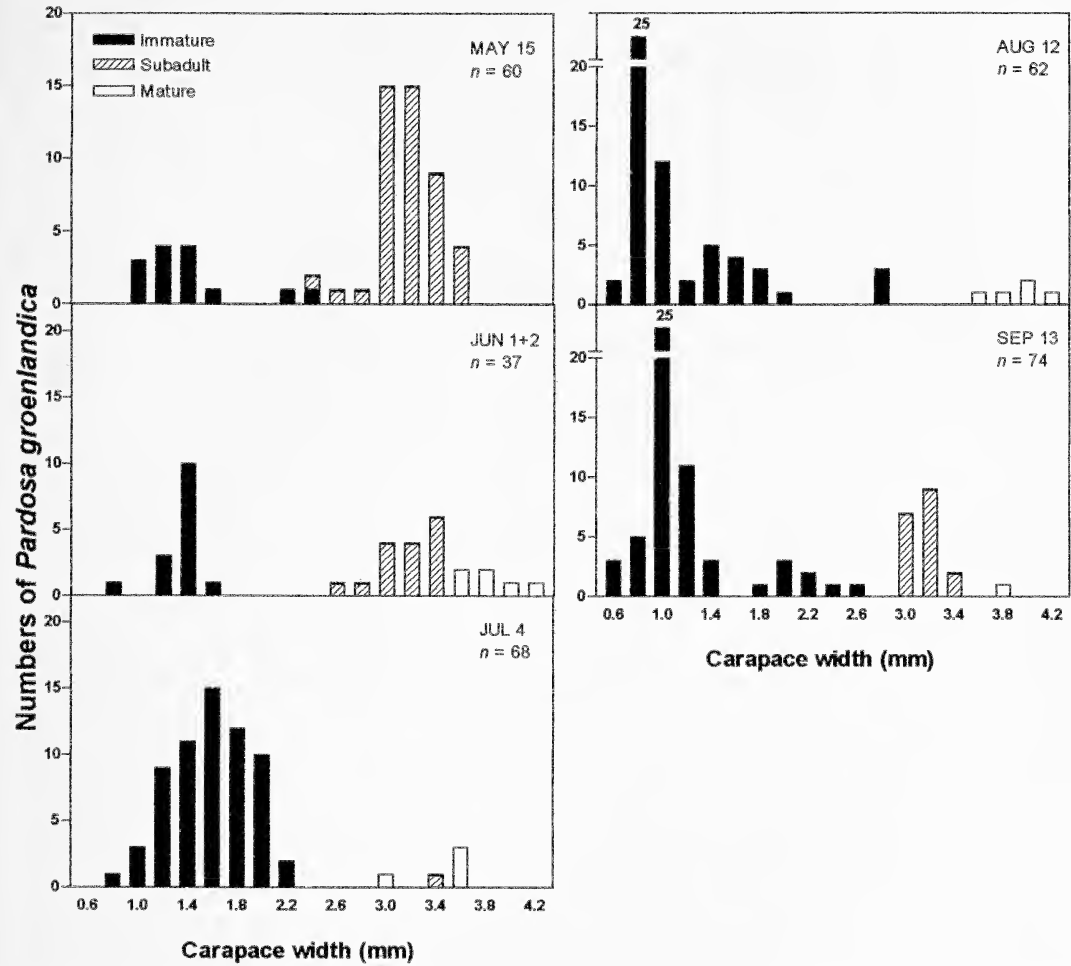
Figure 5.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa groenlandica*.

smaller immatures seen in September (modal CW 1.0 mm) were new spiders hatched the previous month (August) with one month's growth, and the smallest of this group may be a few new spiders hatched in September. The larger immatures (modal CW 1.9 mm) are seen as persistent juveniles from the previous year that were not large enough to become subadults, possibly in combination with some slightly older individuals hatched the previous month.

DISCUSSION

Measurements.—Since measurements of CW and tibia I yielded essentially the same information either could have been used here. However, CW was adopted because it was easier to manipulate the carapace into position for measurement. This is contrary to the opinion of Toft (1976) who argued that tibia I was easier to measure and used a linyphiid as an example. No doubt this discrepancy is due to the morphology of the taxa under consideration: what is true for lycosids may not be true for linyphiids. The use of CW to establish life-cycle stages has frequently been reported, for example by Almquist (1969), Workman (1978) and Putman (1967).

Life-cycles.—The four life-cycles demonstrated here are essentially similar to biennial species elsewhere, for example *P. lugubris* in Scotland (Edgar 1971a), *Trochosa ruricola* in Finland (Hackman 1957), *P. moesta* and *P. mackenziana* (Keyserling 1877) in Alberta
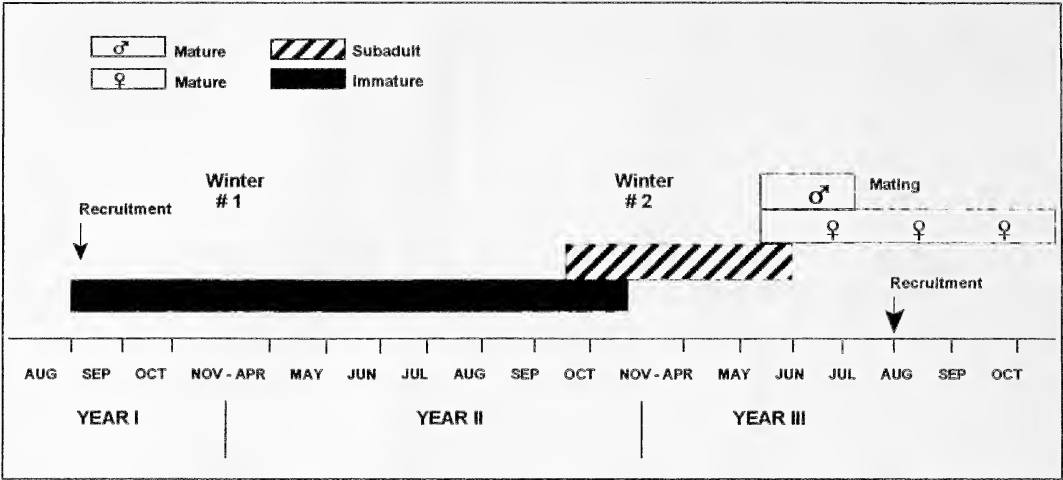
Figure 6.—Generalized life-cycle of *Pardosa moesta, Pardosa hyperborea, Pardosa fuscula* and *Pardosa groenlandica* on the Island of Newfoundland, Canada.

(Buddle 2000), *Dolomedes fimbriatus* in Finland (Palmgren 1939) and *D. triton* (Walckenaer 1837) in Alberta (Zimmermann & Spence 1998), *Philodromus rufus* and *P. cespitum* in Nova Scotia (Dondale 1961), *Araniella displicata* in Nova Scotia (Dondale 1961) and *Eris militaris* in Nova Scotia (Dondale 1961). Others, such as the three British species of *Amaurobius,* are biennials but the second overwintering is as adults not as older immatures (Cloudsley-Thompson 1955).

Pardosa moesta is the only one of the present four investigated elsewhere, and the biennial life-cycle of this species in Alberta (Buddle 2000) differs from the present work only in detail. In Alberta mating was mid-May to early June (July in Newfoundland) and cocoon-carrying early June through August (principally August and September in Newfoundland). These differences can be attributed to climate. In Alberta the population lived in the boreal transition ecoregion dominated by hardwoods with a mean annual precipitation of ca. 500 mm and the following mean temperatures: annual 1°C, summer 14°C and winter −13.5°C. The Newfoundland population lived in the northern peninsula ecoregion dominated by conifers with a mean annual precipitation of ca. 1150 mm and the following mean temperatures: annual 3°C, summer 11°C and winter −4.5°C (Ecological Stratification Working Group 1995).

Apart from these generalizations, at least two of the present four species had a longer period of recruitment than immediately apparent from the data. Within the sampling period (which ended mid September) all species showed one recruitment of new spiderlings: *P. fuscula* and *P. moesta* in September and *P. hyperborea* and *P. groenlandica* in August. However, a significant number of *P. hyperborea* and *P. moesta* in September carried cocoons that would have hatched after sampling stopped. The single *P. groenlandica* female (with a cocoon) caught in September is not an adequate basis for further discussion. Whether such an extended period was due to females carrying single cocoons over a longer period or to some females carrying more than one cocoon, whether this might be expressed bimodally, and the implications of this for both synchrony of the sexes and the size range of the life-stages will be discussed below.

Production of two or more cocoons by one female over an extended period has been reported for several lycosids. Some reports were based on the direct evidence of marking techniques (e.g. Vlijm et al. 1963 for *P. amentata* (Clerck 1757), *P. monticola* (Clerck 1757), and *P. nigriceps* (Thorell 1856) in the Netherlands) . Others were based on indirect evidence such as length of the cocoon-carrying season (e.g. Eason (1969) for *P. lapidicina* Emerton 1885 in Arkansas; Vlijm & Kessler-Geschiere (1967) for *P. pullata* (Clerck 1757), *P. nigriceps* and *P. monticola* in the Nether-

lands; Edgar (1971a) for *P. lugubris* in Scotland; Tóth *et al.* (1997) for *P. agrestis* (Westring 1862) in Hungary). These species all had an early start to mating followed by a minimum four-month cocoon-carrying season, but there are suggestions of two cocoons in a shorter period. For example, both Wolff (1981) for *P. moesta* and Buddle (2000) for *P. moesta* and *P. mackenziana* surmised that a second cocoon was likely because they were carried over 3 mo. In the present study there is only the indirect evidence of duration and late start of the cocoon-carrying season to indicate how many cocoons females carried. None of the four species here had cocoons before July, whereas they were typically seen in May or at latest June in reports of two cocoons elsewhere. The cocoon-carrying periods of all four present species seem shorter than reported elsewhere, but there was an unobserved, extended cocoon-carrying season for at least two species after sampling stopped in September as discussed above. Overall, the late start and shortness of the cocoon-carrying season suggest that second cocoons were not usual. But whether from one cocoon or two, *P. moesta* and *P. hyperborea* had extended recruitment periods. These might result in bimodal recruitment and they have implications for both synchrony of the sexes and the range of sizes of life-stages.

One type of bimodality was reported by Samu et al. (1998) in *P. agrestis,* where a long reproductive period had synchronous peaks of males and females in May and August, each preceded by a peak of subadults, with new spiderlings present from early June to October. The present study is clearly distinguished by the shortness of the cocoon-carrying period, the late start to mating and the lack of a double peak of subadults. However, there may be an unobserved, bimodal peak in recruitment produced by late hatching cocoons as predicted by Edgar (1971b) for *P. lugubris* in Scotland.

An extended recruitment period could affect synchrony because some late-hatched spiderlings might not mature in concert with the majority of immatures that have just overwintered for the second time. Therefore some individuals could be triennial, taking an extra year to mature, as reported for *Trochosa terricola* (Workman 1978). This might explain the presence in July and early appearance in

September of subadult *P. groenlandica,* the presence of small immature *P. groenlandica* in June and July, and the large immature *P. hyperborea* embedded among the adults in September. On the other hand, Edgar (1971b) showed that late hatched spiderlings rapidly catch up in size with their counterparts from an early hatch, thereby reducing or obliterating the anticipated bimodal age distribution of these two cohorts.

The wide variation in size-range of life-stages seen in the present study has been reported for other lycosids, for example by Eason & Whitcomb (1965), Almquist (1969) and Eason (1969). An extended period of recruitment would increase the number of instars occurring together, which would increase the size-range of life-stages, particularly the immatures that contain several instars. There may also be differences between early and late-hatched spiderlings. Edgar (1971b) reported that later spiderlings tended to be heavier than earlier (but whether heavier equals a larger CW is uncertain). On the other hand, Buddle (2000) said that later spiderlings were substantially smaller than earlier. Against this must be balanced the report that later spiderlings tend to catch up with earlier ones (Edgar 1971b). Either way, size difference of new spiderlings will to an extent increase the spread of the size-range of subsequent life-stages, particularly of the immatures. Overall, such variations in size do not obscure the general conclusions of the present work, but may mask subtle attributes of the populations.

The present work has increased the knowledge of spider life-cycles in northern localities, compared these four species to other biennials, and suggested that some individuals may extend their life-cycle beyond 2 yr. The question of whether and to what extent spiders can extend their life-cycles to accommodate increasingly difficult environmental conditions awaits further studies at more northern latitudes or perhaps higher elevations.

LITERATURE CITED

Almquist, S. 1969. Seasonal growth of some dune-living spiders. Oikos 20: 392–408.

Berghe, Van den E. 1992. On pitfall trapping invertebrates. Entomological News 103:149–156.

Buddle, C.M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. Journal of Arachnology 28: 319–328.

Cloudsley-Thompson, J.L. 1955. The life-histories of the British cribellate spiders of the genus *Ciniflo* Bl. (Dictynidae). Annals and Magazine of Natural History 8:787–794.

Dondale, C.D. 1961. Life histories of some common spiders from trees and shrubs in Nova Scotia. Canadian Journal of Zoology 39:777–787.

Dondale, C.D. 1977. Life histories and distribution patterns of hunting spiders (Araneae) in an Ontario meadow. Journal of Arachnology 4:73–93.

Dondale, C.D. 1999. Revision of the *groenlandica* subgroup of the genus *Pardosa* (Araneae, Lycosidae). Journal of Arachnology 27:435–448.

Dondale, C.D. & J.H. Redner. 1990. The Wolf Spiders, Nurseryweb Spiders, and Lynx Spiders of Canada and Alaska. Araneae: Lycosidae, Pisauridae, and Oxyopidae. The Insects and Arachnids of Canada Part 17. Agriculture Canada Publications 1856. 383 pp.

Eason, R.R. 1969. Life history and behavior of *Pardosa lapidicina* Emerton (Araneae: Lycosidae). Journal of the Kansas Entomological Society 42: 339–360.

Eason, R. & W.H. Whitcomb. 1965. Life history of the dotted wolf spider, *Lycosa punctulata* Hentz (Araneida: Lycosidae). Arkansas Academy of Science Proceedings 19: 11–20.

Edgar, W.D. 1971a. The life-cycle, abundance and seasonal movement of the wolf spider, *Lycosa* (*Pardosa*) *lugubris,* in central Scotland. Journal of Animal Ecology 40: 303–322.

Edgar, W.D. 1971b. Seasonal weight changes, age structure, natality and mortality in the wolf spider *Pardosa lugubris* Walck. in central Scotland. Oikos 22: 84–92.

Edgar, W.D. 1972. The life-cycle of the wolf spider *Pardosa lugubris* in Holland. Journal of Zoology London 168: 1–7.

Ecological Stratification Working Group. 1995. A National Ecological Framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa/Hull. 125 pp.

Emerton, J.H. 1902. The Common Spiders of the United States. Ginn and Company, Boston. 235 pp.

Hackman, W. 1954. The Spiders of Newfoundland. Acta Zoologica Fennica 79:1–99.

Hackman, W. 1957. Studies on the ecology of the wolf spider *Trochosa ruricola* Deg. Commentationes Biologicae 16 (6):1–34.

Hagstrum, D.W. 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and the field. Annals of the Entomological Society of America 64:757–760.

Leech, R.E. 1966. The spiders (Araneida) of Hazen Camp 81°49′N, 71°18′W. Quaestiones Entomologicae 2:153–212.

Palmgren, P. 1939. Ökologische und physiologische Untersuchungen uber die Spinne *Dolomedes fimbriatus* (Cl.). Acta Zoologica Fennica 24:1–42.

Putman, W.L. 1967. Life histories and habits of two species of *Philodromus* (Araneida: Thomisidae) in Ontario. Canadian Entomologist 99:622–631.

Ricards, D.R. 1967. An investigation of the ecology of the wolf spider *Pardosa groenlandica* Th. (Araneae, Lycosidae). Unpublished M.A.Thesis, University of Montana, Bozeman.138pp.

Samu, F., J. Németh, F. Tóth, E. Szita, B. Kiss, & C. Szinetár. 1998. Are two cohorts responsible for the bimodal life-history pattern in the wolf spider *Pardosa agrestis* in Hungary? *In* Seldon, P. A. (ed.). Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. Pp. 215–221.

Schmoller, R. 1970. Life histories of alpine tundra arachnida in Colorado. American Midland Naturalist 83:119–133.

South, G.R. (Ed). 1983. Biogeography and Ecology of the Island of Newfoundland. W. Junk, Hague. 723 pp.

Stratton, G.E. & D.C. Lowrie. 1984. Courtship behavior and life cycle of the wolf spider *Schizocosa mccooki* (Araneae, Lycosidae). Journal of Arachnology 12:223–228.

Toft, S. 1976. Life-histories of spiders in a Danish beech wood. Natura Jutlandica 19:5–40.

Toft, S. 1979. Life histories of eight Danish wetland spiders. Entomologiske Meddelelser 47:22–32.

Topping, C.J. & K.D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29: 485–491.

Tóth, F., J. Kiss, & B. Bálint. 1997. Reproduction characteristics of *Pardosa agrestis* (Westring) (Araneae, Lycosidae) based on pitfall trappiong in winter wheat. Acta Phytopathologica et Entomologica Hungarica 32: 313–317.

Vlijm, L. & A.M. Kessler-Geschiere. 1967. The phenology and habitat of *Pardosa monticola, P. nigriceps* and *P. pullata* (Araneae, Lycosidae). Journal of Animal Ecology 36: 31–56.

Vlijm, L., A. Kessler & C.J.J. Richter. 1963. The life history of *Pardosa amentata* (Cl.) (Araneae, Lycosidae). Entomologische Berichten Amsterdam 23: 75–80.

Wolff, R.J. 1981. Wolf spiders of the genus *Pardosa* (Araneae: Lycosidae) in Michigan. Great Lakes Entomologist 14: 63–68.

Workman, C. 1978. Life cycle and population dynamics of *Trochosa terricola* Thorell (Araneae: Lycosidae) in a Norfolk grass heath. Ecological Entomology 3:329–340.

Zimmermann, M. & J. R. Spence. 1998. Phenology and life-cycle regulation of the fishing spider *Dolomedes triton* Walckenaer (Araneae, Pisauridae) in central Alberta. Canadian Journal of Zoology 76:295–309.

SYNONYMS OF *FRONTINELLA TIBIALIS* (ARANEAE, LINYPHIIDAE)

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ABSTRACT. Synonymy among three species of linyphid spiders of the genus *Frontinella* F. O. Pickard-Cambridge 1902 is established based on field association between males and females, mating records, and morphological data from recently collected specimens. It is concluded that *F. caudata* Gertsch & Davis 1946 and *F. lepidula* Gertsch & Davis 1946 are both junior synonyms of *F. tibialis* F. O. Pickard-Cambridge 1902. A redescription of this species is included.

RESUMEN. Se establece la sinonimia entre tres especies de arañas linífidas del género *Frontinella* F. O. Pickard-Cambridge 1902, con base en datos de campo sobre la asociación entre machos y hembras, registros de apareamientos, y datos de la morfología de especimenes recientemente colectados. Se concluye que *F. caudata* Gertsch & Davis 1946 y *F. lepidula* Gertsch & Davis 1946 son sinónimos junior de *F. tibialis* F. O. Pickard-Cambridge 1902. Se incluye una redescripción de esta especie.

Keywords: Linyphiidae, *Frontinella*, synonymy, Mexico, Chiapas.

The spider genus *Frontinella* was created by F. O. Pickard-Cambridge in 1902 for eight species found in Central and North America. Petrunkevitch (1911) made *Frontinella* a junior synonym of *Linyphia* Latreille 1804 without argument, but Blauvelt (1936) resurrected *Frontinella* from this synonymy when she made a revision of *Linyphia* and several related genera. Roewer (1942, 1954) and Bonnet (1956, 1957), in their respective catalogues, included *Frontinella* as a junior synonym of *Linyphia,* but they did not give any argument. Nevertheless, from that time on most authors considered *Frontinella* a valid genus name (Kaston 1938, 1948; Gertsch & Jellison 1939; Muma 1943; Brignoli 1983; Millidge 1984; Platnick 1989, 1993, 1997; Breene et al. 1993), and several new species were described (Gertsch & Davis 1946; Bryant 1948; Kraus 1955; Li & Song 1993). Millidge (1991) transferred *F. uncata* F. O. Pickard-Cambridge 1902 to the genus *Novafrontina* Millidge 1991. At present there are 15 species worldwide, two from China and 13 from the Americas, with nine of these species reported from Mexico: *F. communis* (Hentz 1850), *F. laeta* (O. Pickard-Cambridge 1898), *F. bicuspis* F. O. Pickard-Cambridge 1902, *F. rustica* F. O. Pick-

ard-Cambridge 1902, *F. tibialis* F. O. Pickard-Cambridge 1902, *F. caudata* Gertsch & Davis 1946, *F. huachuca benevola* Gertsch & Davis 1946, *F. lepidula* Gertsch & Davis 1946 and *F. potosia* Gertsch & Davis 1946. Only two of these have been recorded for the state of Chiapas, Mexico: *F. caudata* and *F. lepidula* (Gertsch & Davis 1946; Hoffmann 1976).

In 1995, we collected female and male specimens of *Frontinella* in coffee plantations in southeast Chiapas. The female specimens were identified as *F. caudata,* some males as *F. tibialis,* and other males as *F. lepidula. Frontinella tibialis* and *F. lepidula* were described from only one male specimen each, *F. caudata* was described from only female specimens. We found accompanying males in the webs of several *F. caudata* females. Most of these were identified as *F. tibialis,* one as *F. lepidula.* The finding of these pairs suggests synonymy.

In their description of *F. lepidula,* Gertsch & Davis (1946) considered it near to *F. tibialis* but pointed out some differences: "This is a smaller species than *tibialis* Cambridge. The embolus of the male palpus is shorter and less strongly curved at the apex, and the pa-

tella of the palpus is armed with a long curved spine instead of a short spur." Some of our male specimens could not be assigned to any of these two species because they have a "short spur" in one patella and a "long spine" in the other, showing another indication of possible synonymy. Thus, we decided to collect more specimens of both sexes, to study and clarify the taxonomy of the three described species.

METHODS

The collecting site was the coffee plantation of the "Campo Agrícola Experimental Rosario Izapa" of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Municipio of Tuxtla Chico, 20 km NNE of Tapachula, Chiapas, at 400 m elevation. This place was selected due to the abundance of *Frontinella*. The first collecting period was from September–November 1995, and the second in January 1998. The spiders were collected by visual search of the webs of adult and subadult females (as it is difficult to differentiate these two age classes in the field); additionally, some solitary males were collected to have enough specimens for the taxonomic study. All individuals found on the same web were put in the same container and preserved in 70% ethanol. In the laboratory each specimen was tentatively identified and the age class and sex was determined. Specimens were deposited at the Colección de Arañas del Sureste de México (ECOTA-AR, El Colegio de la Frontera Sur, Tapachula, Chiapas, Mexico), the American Museum of Natural History, New York (AMNH), and The Natural History Museum, London (NHM).

To study the specimens, we considered the characters in the original description of each species. All adults (females and males) were measured to compare their variability in relation to the measurements of the corresponding type as noted in the original descriptions. The measured characters were total length, carapace length, carapace width, and length of each segment of the first leg from femur to tarsus. Specimens of both sexes were sent to Dr. N. I. Platnick (AMNH), and to Mr. P. D. Hillyard (NHM), for comparison with the corresponding types in those museums. The paratypes of *F. caudata* and of *F. huachuca benevola,* deposited in the Colección Nacional de Arácnidos (CNAN, Dr.Tila María Pérez,

Instituto de Biología, Universidad Nacional Autónoma de México), were also examined for comparative analyses. We examined the patellar macroseta of both palpi for each collected male, and made some SEM photographs of them. Additional information about the type specimens, not included in the original descriptions, was provided by Dr. N. I. Platnick and by Mr. P. D. Hillyard. The descriptions in the taxonomic section were based on the specimens collected in this work, with each measurement noted as average and range of variation (minimum and maximum); all measurements are in millimeters. Abbreviations used in text: ALE: anterior lateral eyes; AME: anterior median eyes; PLE: posterior lateral eyes; PME: posterior median eyes. Fe-I (II, III, IV): first femora (second, third, fourth); Me-I (II, III, IV): first metatarsi (second, third, fourth); Pa-I (II, III, IV): first patellae (second, third, fourth); Ta-I (II, III, IV): first tarsi (second, third, fourth); Ti-I (II, III, IV): first tibiae (second, third, fourth). Cy: cymbium; PCy: paracymbium.

RESULTS

We collected 76 individuals from 55 webs: 39 webs were occupied by only one individual (solitaries), the remaining 16 webs contained 37 spiders, from two to five individuals per web (Table 1). Most accompanied adult females shared the web with only one male, but a few were found with several males. Most sub-adult females were alone on their webs, only one was found with a male. Inexplicably, one sub-adult female and one juvenile were found each on the web of an adult female. Most males were found on the webs of adult females, but two males were each on the web of a juvenile (Table 1).

In one web, one adult female was found with four males (Table 2), and we observed the end of copulation between one of these males and the female. On a date subsequent to the sampling period, one of the authors (J. A. García) observed another pair in a web, copulating at least two times during the 30 min of observation.

The measurements from 30 collected females showed that most mean values of these females are slightly smaller than those of the *F. caudata* holotype and paratype, but the variation of these types are well inside the variation ranges of the collected females. Besides

Table 1.—Numbers of specimens collected on each web, with their corresponding sex/age. F = female(s), M = male(s).

	Adult F	Sub-adult F	Adult M	Juveniles	No. in web totals
Solitaries	18	14	7		39
with F		1	16	1	18
with 1 M	8	1		2	11
with >1 M	3				3
with sub-adult F	1		1		2
with juveniles	1		2		3
Age/sex totals	31	16	26	3	76

the size variations, the study of the adult females showed no major differences among them, nor in respect to the characters noted in the description of *F. caudata,* or those observed in the paratype of this species. The epigyna were very similar for all females, paratype included, in respect to form and position of the openings, dorsal and ventral plates (as defined by Millidge 1984). Although some variability was recorded in the form and size of the opisthosoma and its caudal tubercle, this could be due to differences in nutritional condition, level of development of ovaries, or natural variability.

Gertsch & Davis (1946) considered the length of the patellar macroseta, and length and curvature of the embolus as distinctive characteristics between *F. tibialis* and *F. lepidula.* The collected male specimens showed only slight variability among them in embolus characteristics. On the contrary, for the length of the patellar macroseta we found two states, the "short spur" of Gertsch & Davis (as in the figs. 7a and 7b of *F. tibialis* by F. O. Pickard-Cambridge 1902, table XL), or the "long spine" (as in fig. 11 of *F. lepidula* by Gertsch & Davis 1946).

We found males with "long spines" on both palpi, males with "short spurs" on both palpi, but also males with a "short spur" on one palp and a "long spine" on the other (Table 2). This mixed condition seems to indicate that the macroseta is originally long, but it can break and lose its slender distal part, with only the thick base remaining. SEM images showed that the "short spur" is a patellar macroseta broken in the area where its diameter is reduced (Figs. 1, 2).

Our data also show that both solitary and courting males (in the web of a female) show the three conditions. Likewise, one female specimen was accompanied with males showing these three conditions (Table 2). Also, the male observed copulating with a female on a date subsequent to the collect period had a broken macroseta in one palp and a complete macroseta in the other.

As for the females, the measurements of the collected male specimens showed also overlapping ranges of size among them, and with the holotype of *F. lepidula.* It was also found that the collected males have a mastidion on each chelicera (one small laterally directed tubercle at the anterior proximal surface of the

Table 2.—Numbers of specimens collected alone or accompanied, and the pedipalp-patella macrosetae condition of the corresponding males. F = female, M = male(s), BM = broken macroseta, CM = complete macroseta. * The values with the same subscript letter corresponds to the same female specimen.

	M with 2 CM	M with 2 BM	M with 1 CM and 1 BM
Solitary M	2	2	3
1 F with 1 M	2	4	2
1 F with > 1 M*	$2_b + 1_c$	$2_a + 1_b + 1_c$	1_b
1 subadult F with 1 M	1		
1 juvenile F with 1 M		2	
Totals	8	12	6

cheliceral base, just below the clypeus). The mastidion size is variable, from sharply pointed in some specimens to blunt and very reduced in others. Some specimens have mastidia of different size, one pointed and one reduced. In some of the males, the chelicerae were so retracted that the mastidion was not directly visible because it was covered by the clypeus, but a careful examination showed its presence in all collected males.

DISCUSSION

In some linyphiid species, the males respond to a species-specific sex pheromone present in the silk of adult female webs by approaching the female and initiating courtship behavior; in some cases the males can stay in the web for some time, and even copulate several times with the female (Rovner 1968; Austad 1982; Suter & Renkes 1982; Watson 1986, 1995; Wiley-Robertson & Adler 1994). The presence of the males in the females' webs, and the copulations observed constitute sound evidence of conspecificity, especially since no other related species were found at the collecting site.

The morphological similarity between the collected females and the paratype of *F. caudata* (especially with regard to the epigynum), and the fact that the measurements of the holotype and paratype of this species are inside the ranges of the collected females, indicate that *F. caudata* and the collected specimens are the same species.

Platnick (pers. comm.) considered a female specimen sent to him as the same species as the *F. caudata* holotype, and the male specimens sent to him as the same species of the *F. lepidula* holotype. For the male specimens sent to be compared with *F. tibialis,* Hillyard (pers. comm.) considered that "the pedipalp macroseta is not significantly different", but that "there is some doubt that these two species are conspecific", because he noted some differences such as total length ("the type is slightly larger"), the size of the palp ("more robust in the type"), the shape of the embolus (broader and more curved at its tip), and the presence of mastidia ("the type does not have a single mastidion on the basal segment of each chelicera").

In the original description of *F. tibialis,* F. O. Pickard-Cambridge (1902) noted only the total length, which is not a reliable character

because of the variability of the opisthosomal size in spiders (Blauvelt 1936; Hormiga 1994a). It was not possible to obtain other measurements from this type. Nevertheless, the maximum value of total length found from our specimens is only slightly below of that noted for the type of *F. tibialis* (4.4 vs. 4.5). Additionally, there is a high variability in size in the collected male specimens, where the smallest male is only one half of the largest (2.2 to 4.4). Furthermore, the range of variation for each measured character overlapped among the three variants of the collected males (with 2 complete macroseta, with 2 broken macroseta, and with one complete and one broken macroseta), and the measurements of the *F. lepidula* holotype were also inside these variation ranges. As *F. tibialis* was described from only one specimen, there were no records about its size variability. Thus, the slight difference in size does not contradict the conspecifity of our specimens with the type of *F. tibialis.*

Concerning the differences between *F. tibialis* and *F. lepidula* in size and curvature of the embolus mentioned by Gertsch & Davis (1946), we consider these as minor differences in comparison with other *Frontinella* species (judging from the drawings of F. O. Pickard-Cambridge 1902; Blauvelt 1936; Gertsch & Davis 1946; and Song et al. 1999), where the pedipalpal bulbs (subtegulum, tegulum, embolic division, particularly the embolus and lamella characteristica) are conspicuously different among species. When the palpal bulb of the collected specimens is observed from different angles the embolus becomes more or less curved, and the lamella characteristica becomes more or less wide. Additionally, the type of *F. tibialis* comes from a locality near the Gulf of Mexico coast, but the type of *F. lepidula* and the males we collected come from a locality near the Pacific coast of Mexico; therefore, it is possible that these are opposite ends of a geographic variability spectrum concerning the size and curvature of the embolus.

F. O. Pickard-Cambridge (1902) noted explicitly in his key to *Frontinella* species that *F. tibialis* lacks mastidia, but all our male specimens have one on each chelicera, although sometimes a very reduced one. The presence of mastidia was not mentioned by Gertsch & Davis (1946), but Platnick (pers.

comm.) confirmed its presence in the *F. lep-idula* holotype. Most species of *Frontinella* with known males have a mastidion on their chelicerae: *F. laeta* and *F. bicuspis* (F. O. Pickard-Cambridge 1902), *F. communis* (Blauvelt 1936), *F. huachuca* and *F. huachuca benevola* (Platnick pers. comm. and personal observation of the male paratype of *F. huachuca benevola* in the CNAN). Thus, the presence of mastidia seems not to be rare in this genus. The collected male specimens showed a high variability in the size of their mastidia. As *F. tibialis* was described from only one specimen, there were no records about mastidion variability. Also, it is possible that this difference corresponds to a spectrum of variability between the two populations (Gulf coast and Pacific coast).

Gertsch & Davis (1946) said about *Frontinella,* "It is notable that the males of the three new species herein described all have the patella of the palpus set with a long dorsal spine. In all the other known species this spine is modified into a short spur." As both species, *F. tibialis* and *F. lepidula,* were described each with only one specimen, the variation existing in this character was not observed. We do not know when and how the patellar macroseta breaks. As they are present only in the males, it is possible that these structures are related to reproductive activities. It would be necessary to study the reproductive behavior of this species to know more about the function of this structure.

Other similarities that support the hypothesis of conspecifity between the type of *F. tibialis* and the collected male specimens are the presence of macrosetae in the mesal border of the cymbium (Fig. 7), the relative size between pedipalp's patella and the tibia (tibia about twice as long as patella), the form of the pedipalp's tibia (widening to its distal end, Figs. 6–8), and the form of the male sternum, narrowly produced between coxae IV (as in table XL, fig. 7 of F. O. Pickard-Cambridge 1902).

From this evidence, we conclude that *F. caudata* and *F. lepidula* are junior synonyms of *F. tibialis* by the principle of priority (Article 23 of the ICZN). As the original description of *F. tibialis* is very short, we include here a redescription of this species based on the specimens collected in this work.

TAXONOMY
Figs. 1–10
Frontinella tibialis
F. O. Pickard-Cambridge 1902

Frontinella tibialis F. O. Pickard-Cambridge, 1902: 422, plate XL figs. 7a–b ♂; Gertsch & Davis, 1946: 3.

Linyphia tibialis, Petrunkevitch 1911: 255; Roewer 1942: 591; Bonnet 1957: 2531.

Frontinella caudata Gertsch & Davis, 1946: 4, fig. 6 ♀; Brignoli 1983: 294. NEW SYNONYMY.

Frontinella lepidula Gertsch & Davis, 1946: 4–5, figs. 10–11 ♂; Brignoli 1983: 294. NEW SYNONYMY.

Types.—Male holotype of *F. tibialis* from Teapa, Tabasco, Mexico, in the collection of Goodman & Salvin, deposited in NHM (not examined). Female holotype of *F. caudata* from Chilpancingo, Guerrero, Mexico, deposited in the AMNH, female paratypes from Chilpancingo, Guerrero, Mapastepec and Tapachula, Chiapas, Mexico, deposited in the AMNH and in the CNAN (examined). Male holotype of *F. lepidula* from Tonala, Chiapas, Mexico, deposited in the AMNH (not examined).

Diagnosis.—This is a tentative diagnosis, because several species of this genus are known only from one sex, and we did not revise this genus. A possible autapomorphy of this species is the distinctive form of the lamella characteristica in the male pedipalp (Figs. 4, 7), clearly different from that of all other known males. The tibia's relative length, twice as long as the patella in the male pedipalp (Fig. 3), separates this species from most others species with known males (with tibiae less than twice the patella length), except from *F. potosia,* but in *F. potosia* the patellar macroseta of the pedipalp does not have a widened base as in *F. tibialis.* The position of the copulatory openings (on the lateral borders, about at the middle of the distance between the anterior and posterior borders of the dorsal plate, Fig. 9) distinguish this species from most other species with known females (having the copulatory openings on the anterior border of the dorsal plate), except from *F. zhui* Li & Song 1993, but in this species the posterior border of the dorsal plate is notoriously rounded and extended backwards.

Description.—*Male:* (*n* = 26) Total length 3.25 (2.16–4.43), carapace length 1.49 (0.97–1.86), carapace width 0.98 (0.70–1.20). Di-
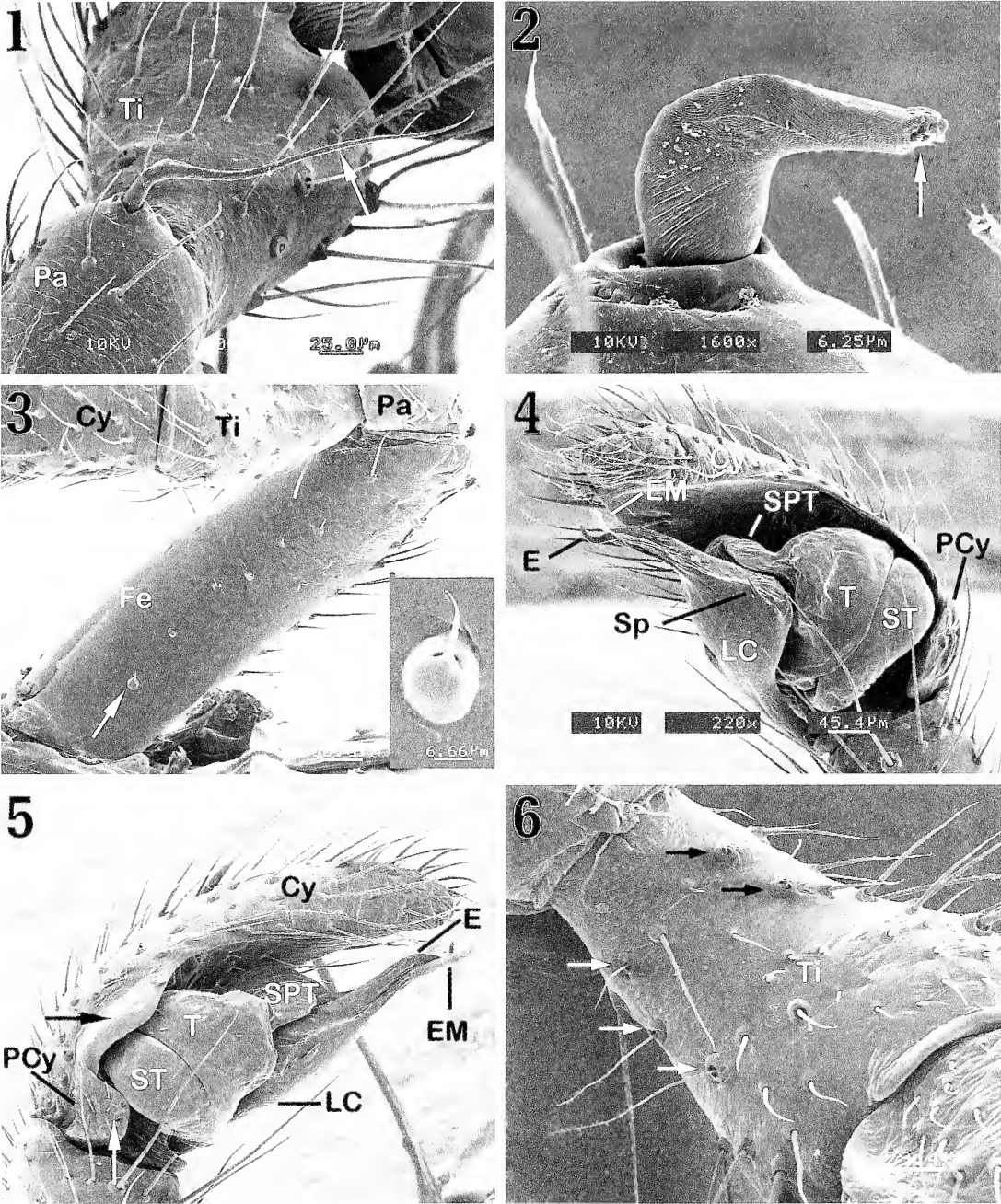
Figures 1–6.—*Frontinella tibialis,* scanning electron micrographs of male pedipalp structures: 1. Complete macroseta of patella; 2. Broken macroseta of patella showing fracture point; 3. Row of setigerous cusps on mesal face of right femur, with enlargement of one cusp (inset) (scale bar for femur 50.0 μm); 4. Ectoventral view of left pedipalp showing visible parts in unexpanded condition; 5. Ectodorsal view of right pedipalp in unexpanded condition showing paracymbium with setae (white arrow) and membrane of cymbium (black arrow) (scale bar 46.5 μm); 6. Dorsal view of right tibia showing three retrolateral (white arrows) and two prolateral (black arrows) trichobothria (scale bar = 29.4 μm). *Abbreviations:* Cy = cymbium; E = embolus; EM = embolic membrane; Fe = femur; LC = lamella characteristica; Pa = patella; Pcy = paracymbium; Sp = spine of lamella characteristica; SPT = suprategulum; ST = subtegulum; T = tegulum; Ti = tibia.
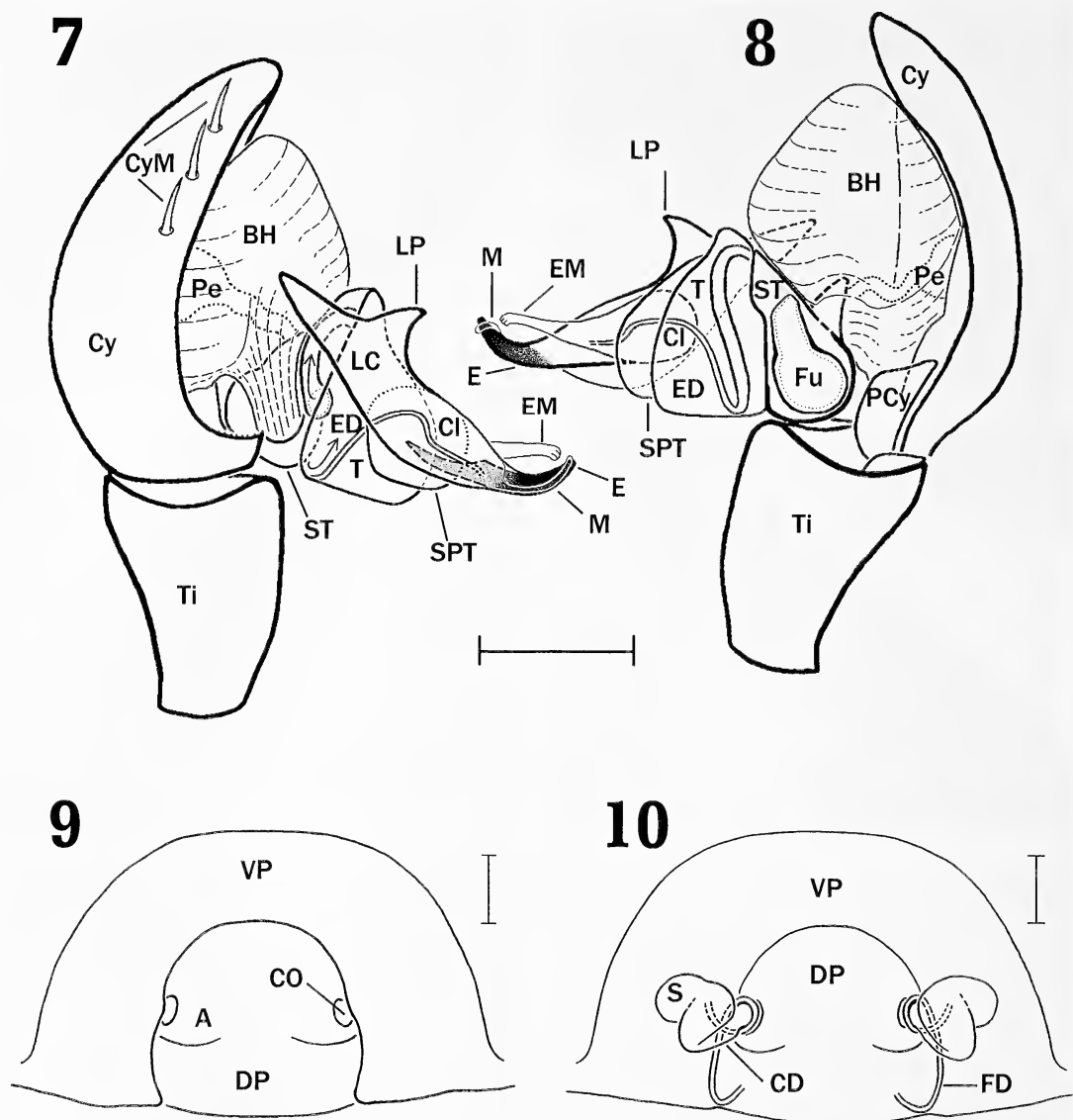
Figures 7–10.—*Frontinella tibialis,* drawings of genitalia. 7–8. Left male pedipalp with expanded bulb. 7. Meso-ventral view; 8. Ecto-dorsal view; 9–10. Female epigynum. 9. Ventral view; 10. Dorsal view of cleared epigynum. Scale bars = 0.1 mm. *Abbreviations:* Pedipalp: BH = basal hematodocha; Cl = column; Cy = cymbium; CyM = cymbium macrosetae; E = embolus; ED = ejaculatory duct; EM = embolic membrane; Fu: = fundus; LC = lamella characteristica; LP = lateral process of lamella characteristica; M = membrane; Pcy = paracymbium; Pe = petiole; SPT = supprategulum; ST = subtegulum; T = tegulum; Ti = tibia. Epigynum: A = atrium; CD = copulatory duct; CO = copulatory opening; DP = dorsal plate; FD = fertilization duct; S = spermatheca; VP = ventral plate.

ameter of AME 0.08 (0.07–0.09), ALE 0.09 (0.07–0.11), PME 0.09 (0.08–0.09), PLE 0.08 (0.07–0.11). Separation between AME 0.06 (0.05–0.07), PME 0.08 (0.07–0.11), AME and ALE 0.11 (0.08–0.13), PME and PLE 0.13 (0.09–0.15). Clypeus height 0.25 (0.19–0.32). Length of Fe-I 2.38 (1.60–3.16), Pa-I 0.39

(0.30–0.50), Ti-I 2.03 (1.40–2.63), Me-I 2.33 (1.60–3.26), Ta-I 1.23 (0.90–1.53), Pa-II 0.35 (0.28–0.43), Ti-II 1.56 (1.08–2.03), Pa-III 0.28 (0.20–0.37), Ti-III 0.81 (0.54–1.07), Pa-IV 0.35 (0.24–0.47), Ti-IV 1.42 (0.94–2.00).

Carapace with a distinct but shallow thoracic groove. Eyes on low tubercles, anterior

eye row moderately recurved, posterior eye row slightly recurved, lateral eyes contiguous. Labium about 1.5 times wider than long, in close contact with sternum. Sternum scutiform, produced behind between coxae IV. Cheliceral base with a narrow but distinct stridulatory band on the ectal side; with a mastidion on the anterior face near to its base, varying from a sharply pointed tubercle to a reduced blunt one; anterior face of chelicerae with scattered setigerous cusps. Chelicerae with 4–5 promarginal teeth and 4–5 small retromarginal teeth. Endites with a diagonal carina on the outer half of the distal border. Legs I-II≈IV-III. Coxae IV separated by about one half of their width; Fe-I to IV with a few longitudinal ventral and lateral series of setigerous cusps, more conspicuous on Fe-I and II. Opisthosoma elongated-oval from above, about twice as long as wide; more or less rectangular in lateral view, with a scarcely developed rounded caudal tubercle.

Pedipalp: Femur with small setigerous cusps on its dorsal, and ectal faces; mesal face smooth with only 5–6 setigerous cusps in a longitudinal line (Fig. 3). Patella with a dorso-distal protuberance that supports a macroseta. Tibia about twice as long as patella (Fig. 3), and widening to its distal end (Figs. 6–8). Cy elongated, about twice as long as maximum wide, narrowing toward its tip, with a translucent, convex membrane on the proximal half of its ectal border; alveolus occupying almost all proximal face, leaving unoccupied about distal one tenth (Figs. 4–5, 7–8). PCy a small curved strip (intersegmental sensu Hormiga 1994b), similar in texture and coloration to Cy, about one sixth the Cy length, and touching the Cy membrane (Figs. 5, 8). Subtegulum transverse; tegulum trapezoidal, narrow on its distal border; suprategulum visible distal to tegulum, between the embolic division and the alveolus (Figs. 4, 5). Embolic division connected to tegulum by a membranous column. Lamella characteristica elongated, proximally directed in the not expanded bulb, pointed on its proximal tip and reaching the base of Cy (Figs. 4); with one short lateral process on its mesal side (Figs. 7, 8), that reaches the middle of the mesal border of Cy, and with an inconspicuous spine (visible only at high magnification, Fig. 4) on the opposite side (the spur of the lamella in Blauvelt's 1936 description of *F. communis*). Embolus pointed and curved

on its apex, more or less parallel to Cy, embolic membrane and membrane both parallel to embolus, ending as membranous strips that touch the embolus tip (Figs. 4, 5, 7 & 8).

Carapace almost glabrous, sternum and endites with sparse setae. Chelicerae with sparse short setae on anterior face, apex of outer sides and a few setae bordering both cheliceral margins. Legs with scattered setae, more numerous and stiff on Me and Ta; stiff setae on setigerous cusps of Fe. Bristles on legs as follows: 2 dorsal on Pa and Ti-I to IV; 1 ventral on Ti-I and II; 1 prolateral on Ti-I; 1 retrolateral on Ti-I and II; 1 dorsal and 1 ventral on Me-III; 1 dorsal on Me-IV. Opisthosoma with sparse, short setae and with two groups of long bristles on its anterior end, above each side of the pedicel.

Pedipalp: with sparse setae form femur to Cy; patella with a long distal dorsal macroseta on dorso-distal protuberance, the macroseta proximal ¼ is thick and curved to the outer side (forming an angle of about 90º from the femur axis), and the rest thin and more or less straight, tapering to a point, (Figs. 1, 2). Tibia with longer setae forming an incomplete ring near its distal border, with 2–3 retrolateral trichobothria and 1–2 prolateral trichobothria (Fig. 6). Cy with 3–4 short thick macrosetae on the distal half of its mesal border (Fig. 7). PCy with a few small setae on its distal half, visible only at high magnification (Fig. 5).

Coloration: Variations observed on both fresh and older preserved specimens. Carapace, chelicerae and endites orange-brown, pars thoracica with faint dusky radiating lines, eye tubercles black. Endites becoming white-yellow towards their tip, with a black carina on the outer half of the distal border. Sternum and labium dusky orange-brown, with borders in front of endites and rear point infuscated. Pedipalpi dusky light-green to dark orange-brown. Legs with coxae to basal two thirds of femora light orange-brown, the rest dusky light-green, darker from tibiae to tarsi. Opisthosoma creamy-gray with dorsal orange-brown tinge, and sides with a dark band and patches. Venter, caudal tubercle and spinnerets darker.

Female: (n = 30) Total length 5.69 (4.46–6.95), carapace length 1.96 (1.47–2.25), carapace width 1.29 (0.87–1.67). Diameter of AME 0.09 (0.08–0.11), ALE 0.12 (0.11–0.13), PME 0.11 (0.09–0.12), PLE 0.10

(0.09–0.11). Separation between AME 0.06 (0.05–0.08), PME 0.09 (0.08–0.11), AME and ALE 0.16 (0.13–0.17), PME and PLE 0.16 (0.11–0.17). Clypeus height 0.25 (0.20–0.29). Length of Fe-I 3.14 (2.56–3.56), Pa-I 0.63 (0.50–0.70), Ti-I 2.91 (2.60–3.30), Me-I 3.11 (2.40–3.55), Ta-I 1.53 (1.13–1.80), Pa-II 0.60 (0.53–0.63), Ti-II 2.25 (1.97–2.43), Pa-III 0.49 (0.43–0.50), Ti-III 1.26 (1.07–1.37), Pa-IV 0.55 (0.50–0.57), Ti-IV 2.20 (1.90–2.40).

Female similar to male except in the following characters: labium not in close contact with sternum. Cheliceral base clearly thickened proximally, without mastidia nor setigerous cusps. Tarsi of pedipalpi with one simple claw. Legs I-IV-II-III. Fe without series of setigerous cusps. Opisthosoma more or less trapezoidal in lateral view, with the rear side higher than the anterior side, and with a pronounced caudal tubercle projected beyond the spinnerets. Opisthosoma with sparse short setae on the ventral plate of epigynum. Carapace and chelicerae brown to dark brown. Sternum, labium and endites dusky brown. Pedipalpi dusky light-green, darker to the tarsi. Legs with distal half of Fe light orange-brown. All Fe with a transverse dark gray band on the distal ventral border. Opisthosoma dark brown to black, some specimens with a pair of small creamy white points on the middle of dorsum. Dorsum margined with an irregular creamy white band including the caudal tubercle, incomplete in some specimens. Sides with another irregular creamy white band at mid-height, and with four transversal (dorso-ventral) irregular discontinuous creamy white bands on the posterior half. With a diffuse patch of creamy white just above the anal tubercle.

Epigynum (Figs. 9, 10) wider than long. Ventral plate slightly convex, protruding very little from the abdominal wall. Dorsal plate about as wide as long, concave in its anterior half forming an epigynal atrium where are found the exposed rounded copulatory openings at each side, touching the border with the ventral plate (Fig. 9). In dorsal view (Fig. 10) copulatory ducts straight and short, pointing to the sides, and leading directly to the spermathecae which are curved, kidney shaped. Fertilization ducts thin, long, leaving spermathecae from the internal curvature to the midline, then making a loop around copulatory ducts, very near to the copulatory openings, and then continuing more or less straight

to the posterior border of the epigynum, in contact with the border between dorsal plate and ventral plate, and curving dorsally at the dorsal border of the genital opening (Fig. 10).

Distribution.—**MEXICO:** *Veracruz* (Potrero), *Tabasco* (Teapa), *Guerrero* (Chilpancingo), and *Chiapas* (Tonala, Mapastepec, Tapachula and Tuxtla Chico).

LITERATURE CITED

Austad, S.N. 1982. First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). Evolution 36 (4):777–785.

Blauvelt, H.H. 1936. The comparative morphology of the secondary sexual organs of *Linyphia* and some related genera, including a revision of the group. Vol. 2, pp. 81–171, *In* Festschrift zum 60 Geburtstage von Professor Dr. Embrik Strand. Riga.

Bonnet, P. 1956. Bibliographia Araneorum. Tome II, 2eme partie: C-F. Toulouse, Les Artisans de L'Imprimerie Douladoure. Pp. 919–1926.

Bonnet, P. 1957. Bibliographia Araneorum. Tome II, 3eme partie: G-M. Toulouse, Les Artisans de L'Imprimerie Douladoure. Pp. 1927–3026.

Breene, R.G., D.A. Dean, M. Nyffeler & G.B. Edwards. 1993. Biology, predation ecology and significance of spiders in Texas cotton ecosystems with a key to the species. Texas Agriculture Experiment Station, College Station (B-1711). 115 pp.

Brignoli, P.M. 1983. A catalogue of the Araneae described between 1940 and 1981. Manchester University Press. 755 pp.

Bryant, E.B. 1948. The spiders of Hispaniola. Bulletin of the Museum of Comparative Zoology 100 (4):331–447.

Gertsch, W.J. & W.L. Jellison. 1939. Notes on a collection of spiders from Montana. American Museum Novitates 1032:1–13.

Gertsch, W.J. & L.I. Davis. 1946. Report on a collection of spiders from Mexico. V. American Museum Novitates 1313:1–11.

Hoffmann, A. 1976. Relación bibliográfica preliminar de las arañas de México (Arachnida: Araneae). Instituto de Biología, Universidad Nacional Autónoma de México, Publicaciones Especiales No. 3. México. 117 pp.

Hormiga, G. 1994a. A revision and cladistic analysis of the spider family Pimoidae (Araneoidea: Araneae). Smithsonian Contributions to Zoology 549:1–104.

Hormiga, G. 1994b. Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae). Zoological Journal of the Linnean Society 111:1–71.

Kaston, B.J. 1938. New spiders from New England with notes on other species. Bulletin of the Brooklyn Entomological Society 33:173–191.

Kaston, B.J. 1948. Spiders of Connecticut. Bulletin of the Connecticut State Geological and Natural History Survey 70:1–874.

Kraus, O. 1955. Spinnen aus El Salvador (Arachnoidea, Araneae). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 493:1–112.

Li, S.Q. & D.X. Song. 1993. On the diagnostic characters of linyphiid spiders, with descriptions of some species (Araneae: Linyphiidae). Scientific Treatise on Systematic and Evolutionary Zoology 2:247–256.

Millidge, A.F. 1984. The taxonomy of the Linyphiidae, based chiefly on the epigynal and tracheal characters (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 6(6):229–267.

Millidge, A.F. 1991. Further linyphiid spiders (Araneae) from South America. Bulletin of the American Museum of Natural History 205:1–199.

Muma, M.H. 1943. Common spiders of Maryland. Natural History Society of Maryland, Baltimore. 179 pp.

Petrunkevitch, A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, Greenland, Bermuda, West Indies, Terra del Fuego, Galapagos, etc. Bulletin of the American Museum of Natural History 29:1–809.

Pickard-Cambridge, F.O. 1897–1905. Arachnida–Araneidea and Opiliones. Vol 2. *In* Biologia Centrali Americana. IX + 610 pp. + 54 plates. London.

Platnick, N.I. 1989. Advances in Spider Taxonomy 1981–1987: A supplement to Brignoli's A catalogue of the Araneae described between 1940 and 1981. Manchester Univ. Press. 673 pp.

Platnick, N.I. 1993. Advances in Spider Taxonomy 1988–1991, With synonymies and transfers 1940–1980. New York Entomological Society. New York. 846 pp.

Platnick, N.I. 1997. Advances in spider taxonomy 1992–1995, With redescriptions 1940–1980. New York Entomological Society. New York. 976 pp.

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. 1 Band. Paul Budy, Bremen. 1040 pp.

Roewer, C.F. 1954. Katalog der Araneae von 1758 bis 1940. 2 Band, Abt. b. Institut Royal des Sciences Naturelles de Belgique, Bruxelles. Pp. 927–1751.

Rovner, J.S. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). Zeitschrift fuer Tierpsychologie 25:232–242.

Song, D., M. Zhu & J. Chen. 1999. The Spiders of China. Hebei Science and Technology Publishing House, Shijiazhuang, China.

Suter, R.B. & G. Renkes. 1982. Linyphiid spider courtship: releaser and attractant functions of a contact sex pheromone. Animal Behaviour 30:714–718.

Watson, P.J. 1986. Transmission of a female sex pheromone thwarted by males in the spider *Linyphia litigiosa* (Linyphiidae). Science 233 (4760):219–221.

Watson, P.J. 1995. Dancing in the dome. Natural History 104(3):40–43.

Wiley-Robertson, M. & P.H. Adler. 1994. Mating behavior of *Florinda coccinea* (Hentz) (Araneae: Linyphiidae). Journal of Insect Behavior 7(3):313–326.

MONOAMINES IN THE BRAIN OF TARANTULAS (*APHONOPELMA HENTZI*) (ARANEAE, THERAPHOSIDAE): DIFFERENCES ASSOCIATED WITH MALE AGONISTIC INTERACTIONS

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ABSTRACT. Experiments were conducted to determine the effects of male-male agonistic encounters on changes in monoamine neurotransmitter concentrations in the supraesophageal ganglion (brain) of the tarantula, *Aphonopelma hentzi*. Serotonin levels were significantly reduced 30 min after fighting in both dominant (66.5 ± 9.1 SE nmol/mg protein) and subordinate (42.8 ± 7.6) animals as compared to isolated controls (89.7 ± 13.2), and these differences persisted for up to 24 h. A similar decrease was found for octopamine concentrations in dominant (43.7 ± 7.7) and subordinate (31.2 ± 4.9) spiders when compared to controls (56.9 ± 5.8). In addition, serotonin and octopamine levels were significantly lower in subordinate vs. dominant spiders. Agonistic interactions had no effect on the concentrations of dopamine, norepinephrine, and epinephrine. In isolated control spiders, serotonin (89.7 ± 13.2 SE nmol/mg protein) was present in highest concentration in the brain, followed by octopamine (56.9 ± 5.8 nmol/mg), dopamine (22.4 ± 3.8 pmol/mg), norepinephrine (15.3 ± 4.7 pmol/mg), and epinephrine (0.57 ± 0.2 pmol/mg). The results indicate that following agonistic encounters, monoamine concentrations in the brain decrease to different levels in winners and losers. This is the first demonstration that the establishment of social status causes changes in brain monoamines in spiders.

Keywords: Agonistic interactions, *Aphonopelma*, CNS monoamines, males

Activation of monoaminergic systems in the central nervous system (CNS) has been implicated in the mediation of short-term and chronic physiological stress responses as well as aggressive and social dominance relationships in numerous taxa (Eichelman 1987; Bicker & Menzel 1989; Haney et al. 1990; Summers et al. 1995). Most of this work has focused on social interactions in vertebrates exposed to staged encounters between conspecifics under laboratory conditions. For example, the social status of subordinate animals is associated with an increase in the utilization of the indolalkylamine neurotransmitter (NT) serotonin (5-HT, 5-hydroxytryptamine) in various brain regions from fish to mammals (Haney et al. 1990; Winberg et al. 1997; Punzo 2000a). In addition, activation of brain catecholaminergic systems including dopamine (DA), norepinephrine (NE), and epinephrine (Epi) in vertebrates is associated with increased levels of aggression and dominance (Eichelman 1987; Matter et al. 1998).

In general, the brain or supraesophageal ganglion (SEG) of arthropods lies above the esophagus and consists of three major brain regions: the protocerebrum, which contains the 'higher brain centers' including the optic lobes and nerves; the central body, corpora pedunculata and a variable number of ganglia and associated neuropils; the deuterocerebrum, which innervates the antennae (reduced in arachnids); and the tritocerebrum, which innervates the mouthparts (Horridge 1965; Gupta 1987). In spiders, the CNS is highly condensed anteriorly, and the SEG consists primarily of the cheliceral and optic nerves, optic neuropils (masses of axonal fiber tracts) for primary and secondary eyes ('corpora pedunculata'), and a loosely organized central body (Babu 1985; Wegerhoff & Breidbach 1995). There have been few studies on neurochemical parameters associated with behavior in general, and agonistic interactions specifically, in arthropods and other invertebrates. For example, increases in protocerebral RNA and protein synthesis have been shown to accompany learning in molluscs (Kerkut et al.

1970; Adamo & Chase 1991), decapod crustaceans (Punzo 1985), insects (Lin & Roelofs 1992; Punzo 1996), and spiders (Punzo 1988a). Cycloheximide-induced inhibition of brain protein synthesis impaired learning and memory in insects (Jaffe 1980) and spiders (Punzo 1988a), as well as innate phototactic behavior in tenebrionid and passalid beetles (Punzo & Jellies 1980). Changes in levels of brain monoamines have been implicated in a variety of ontogenetic shifts in behavior in honeybee workers including the onset of nest-guarding behavior (Moore et al. 1987) and discrimination between olfactory cues (Macmillan & Mercer 1987).

With respect to aggression and agonistic interactions, octopamine turnover rates increased significantly in crickets after fighting with conspecifics (Adamo et al. 1995). Increased foraging activities and nest defense were correlated with higher concentrations of octopamine (OA), dopamine (DA), and serotonin (5-HT) in the SEG of worker honeybees (Harris & Woodring 1992). Indeed, it has been suggested that OA is part of a general arousal system which prepares insects for a variety of vigorous skeletal-muscular activities, territorial defense, and helps the animal deal with stressful conditions (Corbet 1991; Orchard et al. 1993). Increased 5-HT levels in the brain (SEG) have been implicated in the onset of flight behavior in weevils (Guerra et al. 1991). Lobsters exhibiting dominance over conspecifics exhibited higher levels of CNS 5-HT when compared with subordinate animals (Kravitz 1988).

Changes in SEG amine concentrations as well as other NTs were shown to be associated with ontogenetic shifts in behavior in solifugids (Punzo 1993, 1994). First nymphal instars (N1) typically have poorly developed chelicerae, and are gregarious, do not hunt prey, and remain in the nest with their siblings and maternal parent. However, after molting, second-instar nymphs (N2) possess functional chelicerae and become aggressive (Punzo 1998a). They will cannabilize one another if they do not disperse from the nest. This pronounced increase in aggression is associated with significant changes in brain 5-HT and DA levels, although OA levels remained relatively constant throughout postembryonic development (Punzo 1994). In addition, later nymphal instars (N5—N8) exhibited higher brain concentrations of acetylcholine (ACh), norepinephrine (NE), and acetylcholinesterase (AChE) as compared to younger instars (Punzo 1993).

Theraphosid spiders exhibit a variety of aggressive behaviors. Some of these involve male-male agonistic interactions (Baerg 1958; Minch 1977; Punzo & Henderson 1999; Punzo 2000b), while others involve males and females, especially during courtship and mating (Costa & Perez-Miles 1992; Shillington & Verrell 1997), and sometimes end in sexual cannibalism (Punzo & Henderson 1999). A previous study showed that agonistic interactions between paired conspecific males of *Aphonopelma hentzi* (Girard 1854) were observed in 24 out of 27 (88.9%) staged encounters in the laboratory (Punzo & Henderson 1999). These encounters were initiated by vigorous leg-fencing with each protagonist pushing forcefully against its opponent. These fencing bouts were interrupted from time to time with at least one of the males exhibiting a threat display (elevation of the anterior end of the body, first pair of legs and pedipalps, and opening of the fangs). At least one male exhibited a strike response toward his opponent in 11 out of 24 cases (45.8%). In eight of these instances (33.3%), one of the males was killed.

The purpose of this study was to investigate neurochemical parameters associated with agonistic interactions between males of the theraphosid spider, *Aphonopelma hentzi*. Neurotransmitters and comodulators are important regulatory molecules required for the transmission of information (nerve impulses) along neural pathways involved in the control of motor movements as well as 'mood' and motivational states (Ansell & Bradley 1973). Specifically, we were interested in whether or not there were any differences in the concentrations of monoamines (OA, DA, NE, Epi, 5-HT) in the brains (SEG) of dominant ('winners') vs. subordinate ('losers') males following agonistic encounters. To our knowledge, this is the first study to address neurochemical correlates of aggression in spiders.

METHODS

Animals.—Males were collected during July and August of 1997 at a site 3.5 km S of Elgin, Texas (30°32′N, 97°29′W; Bastrop County). This site consisted of a dry wash and surrounding flood plain consisting of sand,

gravel and adobe soils, with numerous rocks, rock crevices, and burrows. The dominant vegetation included prickly pear cactus (*Opuntia*), catclaw (*Mimosa*), mesquite (*Prosopis*), broom weed (*Xauthocephalum*), and mesquite grass (*Bouteloua*). Adult males ranging in size from 4.2–6.7 g were abundant during this period and were easily found moving about the surface between 2000–0300 h (Central Standard Time). Spiders were collected and weighed to the nearest 0.1 g using a Ohaus Model 87 portable electronic balance.

Spiders were transported to the laboratory and housed individually in plastic cages (20 × 16 × 8 cm). They were provided with water *ad libitum* and fed three times per week to satiation on a mixed diet of crickets (*Gryllus* sp.), mealworms (*Tenebrio molitor*), and grasshoppers (*Schistocerca* sp.). They were maintained at 22 °C ± 1°, 65% RH, and a photoperid regime of 12L:12D in a Percival Model 805 environmental chamber (Boone, Iowa). Adult males were kept in these conditions for two weeks and then re-weighed on the day before the initiation of encounter trials. Since previous studies on arachnids have indicated that differences in body size can influence the outcome of aggressive encounters (Faber & Bayliss 1993; Punzo 1998c, 2000b), only males of approximately similar size (6.2–6.7 g) were used for encounter trials and subsequent neurochemical analyses. Voucher specimens have been deposited in the Invertebrate Collection at the University of Tampa.

Encounter trials.—We used a rectilinear glass arena (26 × 16 × 12 cm) divided into halves by an opaque divider to stage conspecific male encounters as described by Punzo (1998c). To summarize, the floor of the arena was provided with a layer of loose sand to a depth of 2 cm. All observations were conducted under Black lighting (BioQuip Onc., Model 2804, Gardena, California). We used a Panasonic PS 150 tape recorder to record verbal descriptions of each encounter.

Before each encounter trial, a male spider (chosen at random) was placed at each end of the arena, separated by the opaque divider. A trial was initiated by removing the divider and allowing the animals to interact. Within a period of time ranging from 0.5–8.5 min over all trials, the contestants made contact with one another (usually with a front leg). In a few trials, one of the spiders would immediately attempt to flee after making initial contact with its opponent. These trials were not used in data analysis. In all other cases ($n = 60$ trials), following initial contact, one of the spiders would begin to push with its front pair of legs against its opponent. The other spider rapidly responded in a similar fashion (leg-fencing). In other cases, after initial contact, one or both spiders would exhibit the threat display, followed by another bout of leg-fencing. In a few instances the fighting escalated until one or both spiders attempted to bite the other. An encounter trial was terminated if at any time during the encounter one of the spiders backed away and rapidly fled from the vicinity of the other spider and attempted to crawl out of the chamber. The spider that held its ground was recorded as the 'winner' (dominant animal), and the spider that fled, the 'loser' (subordinate). Each pair of contestants were subjected to only one encounter trial as described by Summers & Greenberg (1995) in their study of male-male aggression in lizards. We conducted a total of 60 encounter trials comprising 60 pairs of contestants ($n = 120$).

Neurochemical analyses of brain tissues.—Immediately following their designation as dominant or subordinate (based on the outcome of encounter bouts), paired contestants were randomly assigned to one of three groups; each group consisted of 40 spiders (20 pairs). Spiders in group 1 (G1) were anaesthetized with CO_2 thirty min after encounter trials, and their brains (SEG) removed in a cold room, weighed to the nearest 0.1 g on an electronic analytical balance, and frozen at −80°C as described by Punzo (1988b) for subsequent neurochemical analyses. Group 2 (G2) and group 3 (G3) spiders were anaesthetized and their brains frozen at 24 hr and 48 h, respectively, after encounter trials. In this way, we were not only able to determine what neurochemical changes, if any, followed male-male aggression, but also how rapid the response might be, and how long these changes might persist. The brains from another group of 20 spiders (G4) maintained in isolation and not exposed to encounter trials were used as controls.

After thawing, all glandular and peripheral fatty tissue was carefully removed from the surface of the SEG (Murdock & Omar 1981). The SEG were then weighed to the nearest 0.01 g on a Sartorius Model 54C electronic

analytical balance. Brain protein determinations were conducted using the standard procedure described by Lowry et al. (1951) and expressed as percent (brain protein/brain weight) (Meyer et al. 1984). The SEG from the dominant and subordinate spiders were analyzed to determine the concentrations of the monoamine neurotransmitters, 5-HT, OA, DA, and NE, using high performance liquid chromatography with electrical detection (HPLC-ED, Beckman Model 47A) as described by Brandes et al. (1990). To summarize, each brain tissue sample was placed in a 750 μl glass vial and homogenized in 50 μl of a 200 mM perchloric acid (PA) solution. Following homogenization, an additional 50 μl of PA were added to each vial. Samples were then centrifuged at 10,000 g and 4 °C for 3 min in a Sorvall Model 100A high speed refrigerated centrifuge. Twenty μl of supernatant were injected directly into the HPLC column (40 cm in length, with a 0.2 μ pore diameter) packed with Hypersil and provided with a Hewlett-Packard 760E detector (0.40 V). The mobile phase (flow rate, 3000 psi) used to elute the monoamines consisted of 12% acetonitrile, 20 mM sodium acetate, 100 mM sodium dihydrogen orthophosphate, 2.5 mM octane sulfonic acid, and 0.3 mM EDTA disodium salt adjuested to pH 4.2 and filtered through a 0.45 μm filter. Each sample was compared to 5-HT and DA standards tested at the beginning of each assay run and retested at 30 min intervals. Monoamine concentrations were expressed as nmol or pmol/mg protein as desribed by Meyer et al. (1984).

All statistical procedures followed those described by Sokal & Rohlf (1995). Comparisons between mean concentrations of monoamine NTs for the various groups were conducted using an analysis of variance (ANOVA), followed post-hoc by a Duncan's multiple range test at a significance level of 0.05. Significant differences between dominant and subordinate males following aggressive encounters were determined using an independent-samples t test ($P < 0.05$).

RESULTS

Brain weights for all spiders ranged from 8.98–9.32 mg (mean: 9.11 ± 0.56 SE). Brain protein/brain weight (%) ranged from 7.2–7.6. An analysis of variance (ANOVA) indicated that there were no differences in mean brain weights and brain protein values between dominant, subordinate or isolated control spiders ($P < 0.5$). Serotonin was the monoamine found in the highest concentration in the brains of isolated control of *A. hentzi* (Table 1). This was followed in decreasing order by OA, DA, NE, and Epi.

The effects of agonistic interactions between conspecific males on SEG monoamine concentrations at various time intervals following encounter trials are shown in Table 1. Serotonin (5-HT) levels were significantly reduced in spiders losing aggressive encounters (subordinates) for up to 24 h as compared to dominant animals (t = 9.4, $P < 0.01$). This difference persisted for at least 24 h, with levels returning to normal after 48 h (F = 3.36, $P < 0.05$). In addition, the brains of dominant spiders contained significantly lower levels of 5-HT than those of the isolated controls (t = 6.8, P < 0.05) for up to 24 h. These changes in 5-HT and OA levels associated with fighting occurred quite rapidly since changes were detected after only 30 min following an encounter.

A similar pattern was found for OA levels which were also significantly reduced in subordinate vs. dominant animals (t = 6.2, $P < 0.02$). However, the reduced levels of OA associated with agonisitic interactions returned to control levels within 24 hr. With respect to DA, NE, and Epi, no differences were found between spiders exposed to agonistic encounters and controls at any time interval ($P < 0.5$).

DISCUSSION

Although the profile for monoamine concentrations in the SEG of *A. hentzi* (5-HT > OA > DA > NE < Epi) is in general agreement with what little information is available on the neurochemistry of spiders, differences in the NT profiles for spiders from different families have been reported (Florey 1967; Meyer et al. 1984; Meyer 1991) Similar concentrations were reported for NE and DA from the brain of the theraphosid, *Aphonopelma eutylenum* Chamberlin 1918, although no data were presented for 5-HT and OA (Meyer et al. 1984). In contrast, the brain of *Pardosa amentata* (Clerck 1932) contained much higher concentrations of NE (174.9 pmol/mg ± 5.0 SE), a condition most likely associated with the noradrenergic system of the optical

Table 1.—Concentrations of various monoamines (in nmol or pmol/mg protein) in the supraesophageal ganglia (SEG) of *Aphonopelma hentzi* following agonistic interactions between conspecific males. Brain analyses were conducted from tissue extracted from isolated control spiders, as well as from the brains of dominant and subordinant spiders removed 5 min (20 pairs; N = 40) 24 h (*n* = 20 pairs), and 48 h (*n* = 20 pairs) after an encounter trial. Data expressed as means; values in parentheses represent (± SE). Values followed by asterisks are significantly different than controls: ** (*P* < 0.01); * (*P* < 0.05). See text for details.

Neurotransmitter	Controls	Time after encounter		
		5 min	24 h	48 h
Serotonin (5-HT) (nmol/mg)	89.7 (13.2)			
Subordinate		42.8** (7.6)	51.3** (8.3)	92.2 (12.6)
Dominant		66.5* (9.1)	73.9* (10.4)	86.3 (9.5)
Octopamine (nmol/mg)	56.9 (5.8)			
Subordinate		31.2** (4.9)	54.8 (8.1)	60.1 (10.6)
Dominant		43.7* (7.7)	55.3 (5.2)	57.8 (8.2)
Dopamine (pmol/mg)	22.4 (3.8)			
Subordinate		19.6 (5.1)	23.6 (7.1)	21.9 (5.5)
Dominant		22.2 (7.8)	20.6 (3.5)	24.4 (6.2)
Norepinephrine (pmol/mg)	15.3 (4.7)			
Subordinate		18.1 (5.8)	14.3 (2.9)	17.3 (6.6)
Dominant		16.6 (4.4)	18.5 (3.1)	14.9 (4.1)
Epinephrine (pmol/mg)	0.57 (0.2)			
Subordinate		0.61 (0.1)	0.55 (0.2)	0.58 (0.1)
Dominant		0.52 (0.2)	0.63 (0.3)	0.56 (0.2)

brain centers which are more highly developed in salticids (Meyer & Jehnen 1980). Lycosids and agelenids also contained higher levels of DA and NE as compared to theraphosids, although not as high as salticids (Meyer 1991).

The most pronounced changes in monoamine levels involved 5-HT. They occurred among subordinate males 30 min after fighting, although 5-HT levels were reduced in dominant males as well. Thus, fighting between male spiders resulted in a decrease in SEG serotonin levels. To our knowledge, this is the first demonstration of an association between monoaminergic activity and aggression in spiders. Serotonin has been identified with aggressive behavior in other arthropods as well. Injection of 5-HT into lobsters and crayfish caused them to elevate and flex their tails, which represent behavioral acts associated with the expression of dominance (Yeh et al. 1996).

These observations are interesting since a similar reduction in brain serotonin levels accompanying fighting and territorial defense has been reported for a number of vertebrates. Indeed, it has been well established that a variety of stimuli, including social interactions,

activate endocrine stress mechanisms in vertebrates, which are thought to be mediated by changes in CNS neurotransmitters brought about primarily via activation of monoaminergic systems (Ansell & Bradley 1973; Eichelman 1987). For example, Summers & Greenberg (1995) showed that 5-HT levels decreased significantly after one h and one day in the brains (diencephalon and non-optic lobe midbrain) of lizards (*Anolis carolinensis*) losing aggressive interactions. Similarly, no changes were detected for NE and DA levels over this time interval. However, subordinate males exhibited significantly lower DA levels after one week than did subordinates after one h. Changes in the serotonergic content and turnover between individuals of different social status were found in the telencephalon and diencephalon of territorial vs. satellite males in the lizard, *Sceloporus jarrovi* (Matter et al. 1998). In addition, the levels of 5-HT in the telencephalon and diencephalon were found to decrease significantly following male-male aggression in rodents (Haney et al. 1990; White et al. 1991) and fish (Winberg et al. 1997).

Immediately following aggressive defense of territories, territorial male lizards (*S. jar-*

rovi) exhibited higher Epi levels as compared to males that did not experience aggressive encounters (Matter et al. 1998). In contrast, no comparable changes in Epi levels in the SEG of *A. hentzi* were observed after fighting.

Octopamine levels also decreased significantly in males of *A. hentzi* exposed to aggressive interactions. This suggests that an activation of the octopaminergic system, in addition to serotonergic activation, follows aggression in spiders. This is not surprising since OA appears to be central in eliciting the overall arousal response of arthropods (Kravitz 1988; Corbet 1991), and elevated OA activity has been shown to accompany stress (Downer & Hiripi 1993; Harris & Woodring 1992), increased locomotor activity (Orchard et al. 1993; Adamo et al. 1995), courtship (Downer & Hiripi 1993), and a wide range of systemic physiological responses including respiration, gastrointestinal peristalsis, cardio-acceleration, Malpighian tubule filtration, glycogenolysis, and pheromone production (Corbet 1991) in insects. It has been further suggested that certain behavior patterns can be triggered by the activation of specific octo-paminergic pathways in arthropods, an idea known as the 'orchestration hypothesis' (Sombati & Hoyle 1984). For example, administration of exogenous OA has been shown to trigger diurnal hyperactivity in nocturnal moths (Shimizu & Fukamii (1981). Changes in OA levels in the CNS have been associated with ontogenetic shifts in specific behavioral acts in social insects (Bicker & Menzel 1989; Brandes et al. 1990), and an increase in OA activity was found in the brains of crickets following aggressive interactions between conspecifics (Adamo et al. 1995).

Although most of the research on OA has focused on insects, some previous studies, including the present one, suggest that this monoamine plays an important role in regulating the behavior of other arthropods as well. For example, the tail flip response, an integral behavioral component of the escape response of crayfish, is enhanced by OA (Bicker & Menzel 1989). The injection of OA into freely moving lobsters elicited submissive body postures toward conspecifics (Kravitz 1988). The application of OA caused engorged ticks to detach from their hosts (Mason 1986). With respect to OA, direct comparison with vertebrates is not possible since OA has not been identified as a NT in this group.

In conclusion, significant changes in brain concentrations of 5-HT and OA result from male-male agonistic encounters in tarantulas. It has been well established that 5-HT is a CNS monoamine involved in the expression of dominance and aggression in vertebrates, and the results of this study suggest that the establishment of social status in spiders causes changes in brain monoamine levels and may play a role in the elicitation of communicative displays as well. Future studies should focus on other species of spiders as well as other arachnids in order to determine if similar changes in monoamine profiles are associated with aggression in these groups.

ACKNOWLEDGMENTS

LITERATURE CITED

Adamo, S.A., C.E. Linn & R.R. Hoy. 1995. The role of neurohormonal octopamine during 'fight or flight' behavior in the field cricket *Gryllus bimaculatus*. Journal of Experimental Biology 198: 1691–1700.

Adamo, S.A. & R. Chase. 1991. Central arousal and sexual responsiveness in the snail, *Helix aspersa*. Behavioral & Neural Biology 55:194–213.

Ansell, G.B. & P. Bradley. 1973. Macromolecules and Behavior. Univ. Park Press, Maryland.

Babu, K. S. 1985. Patterns of arrangement and connectivity in the central nervous system of arachnids, Pp. 3–19, *In* Neurobiology of Arachnids. (F. G. Barth, ed.). Springer-Verlag, Berlin.

Baerg, W.J. 1958. The Tarantula. University of Kansas Press, Lawrence, Kansas.

Bicker, G. & R. Menzel. 1989. Chemical codes for the control of behavior in arthropods. Nature 337:33–39.

Brandes, C., M. Sugawa & R. Menzel. 1990. High performance liquid chromatography (HPLC) measurement of monoamines in single honeybee brains reveals caste-specific differences between worker bees and queens in *Apis mellifera*. Comparative Biochemestry & Physiology 97C:53–57.

Corbet, S.A. 1991. A fresh look at the arousal syn-

drome of insects. Advances in Invertertebrate Physiology 23:81–116.

Costa, F.G. & F. Perez-Miles. 1992. Notes on mating and reproductive success of *Ceropelma longisternalis* (Araneae, Theraphosidae) in captivity. Journal of Arachnology 20:129–133.

Downer, R.G.H. & L. Hiripi. 1993. Biogenic amines in insects. Pp. 23–38, *In* Insect Neurochemistry and Neurophysiology. (A.B. Borkovek & M.J. Loeb, eds.). CRC Press, Boca Raton, Florida.

Eichelman, B. 1987. Neurochemical and psychopharmacological aspects of aggressive behavior. Pp. 697–704, *In* Psychopharmacology: Third Generation of Progress. (H. Y. Meltzer, ed.). Raven Press, New York.

Faber, D.B. & J.R. Bayliss. 1993. Effects of body size on agonistic encounters between male jumping spiders (Araneae: Salticidae). Animal Behaviour 45:289–299.

Florey, E. 1967. Neurotransmitters and modulators in the animal kingdom. American Society of Experimental Biology 26:1164–1178.

Guerra, A.A. & R.W. Steger & J.C. Guerra. 1991. The possible role of brain serotonin in seasonal dispersal behavior of the boll weevil. Southwestern Entomologist 16:92–98.

Gupta, A.P. 1987. Arthropod Brain: Its Evolution, Development, Structure, and Functions. Wiley Interscience Publs., New York.

Haney, M., K. Noda, K. Kream & K.A. Miczek. 1990. Regional serotonin and dopamine activity: sensitivity to amphetamines and aggressive behavior in mice. Aggessive Behavior 16:259–270.

Harris, J.W. & J. Woodring. 1992. Effects of stress, age, season, and source colony on levels of octopamine, dopamine, and serotonin in the honeybee (*Apis mellifera*) brain. Journal of Insect Physiology 38:29–35.

Horridge, G.A. 1965. Arthropoda: general anatomy, Pp. 801–964, *In* Structure and Function in the Nervous System of Invertebrates. Vol. 2 (T. H. Bullock & G. A. Horridge, eds.). W. H. Freeman, San Francisco, California.

Jaffe, K. 1980. Effects of cycloheximide on protein synthesis and memory in preying mantids. Physiology & Behavior 25:367–371.

Kerkut, G.A., M. French & R. Walker. 1970. The location of axonal pathways of identifiable neurons of *Helix aspersa* using procion yellow M-4R. Comparative Biochemistry & Physiology 32: 681–690.

Kravitz, E.A. 1988. Hormonal control of behavior: amines and the biasing of behavioral output in lobsters. Science 241:1775–1780.

Lin, G. & C. Roelofs. 1992. The effects of biogenic amines on learning in arthropods. Archives of Insect Biochemistry & Physiology 20:359–366.

Lowry, O.H., N.J. Rosebrough, A. Farr & R.J. Randall. 1951. Protein measurement with the folin reagent. Journal of Biological Chemistry 192: 265–275.

Macmillan, C.S. & A.R. Mercer. 1987. An investigation of the role of dopamine in the antennal lobe of the honeybee, *Apis mellifera*. Journal of Comparative Physiology A 160:359–366.

Mason, S.T. 1986. Catecholamines and Behaviour. Cambridge Univ. Press, London.

Matter, J.M., P.J. Ronan & C.H. Summers. 1998. Central monoamines in free-ranging lizards: differences associated with social roles and territoriality. Brain Behavior & Evolution 51:23–32.

Meyer, W. 1991. The biology of excitatory neurotransmitters in the central nervous system of spiders. Histochemistry 59:177–189.

Meyer, W. & R. Jehnen. 1980. The distribution of monoamine oxidase and biogenic monoamines in the central nervous system of spiders (Arachnida: Araneida). Journal of Morphology 164:69–81.

Meyer, W., C. Schlesinger, & H.M. Poehling. 1984. Comparative quantitative aspects of putative neurotransmitters in the central nervous system of spiders (Arachnida: Araneida). Comparative Biochemistry & Physiology 78C:357–362.

Minch, E.W. 1977. The Behavioral Biology of the Tarantula, *Aphonopelma chalcodes*. Ph.D. Dissert., Arizona State University, Tempe, Arizona.

Moore, A.J.M., M.D. Breed & M.J. Moore. 1987. The guard honeybee: ontogeny and behavioral variability of workers performing a specialized task. Animal Behaviour 35:1159–1167.

Murdock, L.L. & D. Oman. 1981. N-acetyldopamine in insect nervous tissue. Insect Biochemistry 11:161–166.

Orchard, I., J. Ramirez & A.B. Lange. 1993. A multifunctional role for octopamine in locust flight. Annual Review of Entomology 38:227–249.

Punzo, F. 1985. Recent advances in behavioral plasticity in insects and decapod crustaceans. Florida Entomologist 68:89–104.

Punzo, F. 1988a. Learning and localization of brain function in the tarantula spider, *Aphonopelma chalcodes* (Orthognatha, Theraphosidae). Comparative Biochemistry & Physiology 89A:465–470.

Punzo, F. 1988b. Physiological amino acids in the central nervous system of the tarantulas, *Aphonopelma chalcodes* and *Dugesiella echina* (Orthognatha: Theraphosidae). Comparative Biochemistry & Physiology 90C:381–383.

Punzo, F. 1993. An analysis of free amino acids, neurotransmitters and enzymes in the nervous system of Solpugida (Arachnida). Comparative Biochemistry & Physiology 106C:699–703.

Punzo, F. 1994. Changes in brain amine concentrations associated with postembryonic development in the solpugid, *Eremobates palpisetulosus*

Fichter (Solpugida, Eremobatidae). Journal of Arachnology 22:1–4.

Punzo, F. 1996. Localization of brain function and neurochemical events associated with learning in insects. Recent Trends in Comparative Biochemistry & Physiology 2:9–16.

Punzo, F. 1998a. The Biology of Camel-Spiders (Arachnida, Solifugae). Kluwer Acad. Publ., Norwell, Massachusetts.

Punzo, F. 1998b. The effects of maternal nest guarding behavior by *Eremobates marathoni* Muma & Brookhart on the survivorship of offspring (Solifugae, Eremobatidae). Bulletin British Arachnological Society 11:54–56.

Punzo, F. 1998c. Intraspecific male aggression in *Arenotherus joshuaensis* Brookhart & Muma, and *Eremobates marathoni* Muma (Solifugae, Eremobatidae). Southwestern Naturalist 43:291–295.

Punzo, F. 2001. Neurochemical correlates of agonistic interactions and dominance between males of the brown anole, *Anolis sagrei*. Florida Scientist, 64:131–139.

Punzo, F. 2000b. Desert Arthropods: Life History Variations. Springer-Verlag, Heidelberg, Germany.

Punzo, F. & L. Henderson. 1999. Aspects of the natural history and behavioral ecology of the tarantula spider *Aphonopelma hentzi* (Girard 1854) (Orthognatha, Theraphosidae). Bulletin British Arachnological Society, 11:121–128.

Punzo, F. & J. Jellies. 1980. Effects of cycloheximide-induced protein synthesis inhibition on the phototactic behavior of *Tenebrio molitor* (Coleoptera: Tenebrionidae) and *Popilius disjunctus* (Coleoptera: Passalidae). Journal of the Kansas Entomological Society 53:597–606.

Shillington, C. & P. Verrell. 1997. Sexual strategies of a North American 'tarantula' (Araneae: Theraphosidae). Ethology 103:588–598.

Shimizu, T. & J. Fukamii. 1981. Role of octopamine in noctuid activity patterns. International Pest Control 23:166–175.

Sokal, B. & R.J. Rohlf. 1995. Biometry. 3rd ed. W. H. Freeman, New York.

Sombati, S. & G. Hoyle. 1984. Generalizations of specific behaviours in a locust by local release into neuropil of the natural neuromodulator octopamine. Journal of Neurobiology 15:481–506.

Summers, C.H. & N. Greenberg. 1995. Activation of central biogenic amines following aggressive interaction in male lizards, *Anolis carolinensis*. Brain Behavior & Evolution 45:339–349.

Wegerhoff, R. & O. Breidbach. 1995. Comparative aspects of the chelicerate nervous system, Pp. 159–179, *In* The Nervous Systems of Invertebrates: An Evolutionary and Comparative Approach. (O. Breidbach & W. Kutsch, eds.). Birkhäuser, Basel, Switzerland.

White, S.M., R.F. Kucharik & J.A. Moyer. 1991. Effects of serotonergic agents on isolation-induced aggression. Pharmacology Biochemistry & Behavior, 39:729–736.

Winberg, S., Y. Winberg & R.D. Fernald. 1997. Effect of social rank on brain monoaminergic activity in cichlid fish. Brain Behavior & Evolution 49:230–236.

Yeh, S., R.A. Fricke & D.H. Edwards. 1996. The effect of social experience on serotonergic modulation of the escape circuit of crayfish. Science 271:366–369.

HABITAT DISTRIBUTION AND LIFE HISTORY OF SPECIES IN THE SPIDER GENERA *THERIDION, RUGATHODES,* AND *WAMBA* IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK (ARANEAE, THERIDIIDAE)

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ABSTRACT. Based largely on 668 one-hour samples collected during a survey of spiders in 16 major habitats of the Great Smoky Mountains National Park, habitat distributions, life history patterns, and other natural history traits are described for 14 species in the related theridiid genera *Theridion, Rugathodes,* and *Wamba.* Two to eight of these species were found in each of the 16 habitats. Among-habitat differences in the kinds and relative abundance of these species suggest that they may be good predictors of habitat. Richness, diversity, and evenness of this species assemblage are highest in middle to low elevation habitats. *Rugathodes aurantius* and *R. sexpunctatus,* two boreal sister species, are abundant in the highest elevation habitats, but differ sharply in microhabitat and habitat preference. *Theridion frondeum* is much more common in high elevation habitats than is its sister species, *T. albidum,* which is virtually limited to middle and low elevation habitats. *Theridion lyricum* is most common in dry, pine-dominated forests. The three most common species (*R. aurantius, R. sexpunctatus,* and *T. frondeum*) have a simple annual life cycle of five or six instars and similar phenologies: they mate during late spring (*R. aurantius* and *R. sexpunctatus*) and early summer (*T. frondeum*) and over-winter in antepenultimate and/or penultimate instars. Female-biased sex ratios were observed in juvenile cohorts of these species. *Rugathodes aurantius,* its natural history previously unknown, places its webs on the undersides of broad-leafed herbs close to the ground and captures small flying insects. Adult females engineer partly folded leaf retreats, carry the egg sac when disturbed, help their instar II spiderlings exit the egg sac, and then share the retreat with these spiderlings for at least a few days. Rapid early development (about two weeks from oviposition to emergence from the egg sac), the presence of females with egg sacs throughout the summer, and smaller clutch sizes in late summer suggest that a typical *R. aurantius* female produces more than one clutch.

Keywords: Spiders, habitat distribution, life history, *Theridion, Rugathodes*

The spider genus *Theridion* Walckenaer 1805, as defined by Levi (1957, 1959, 1963) is cosmopolitan and large (over 90 species have been recorded from North America alone), and many of its species are abundant in favorable habitats. But published knowledge of these species consists of little more than taxonomic descriptions and brief, scattered natural history observations (e.g., Emerton 1902; Archer 1947; Comstock 1948; Levi 1957; Bristowe 1958; Toft 1976; Kaston 1981; Hanggi et al. 1995; Roberts 1995). Moreover, it is now generally accepted that *Theridion* is polyphyletic, and phylogenetic research is underway to determine the relationships of these species (I. Agnarsson & M. Arnedo pers. comm.). Wunderlich (1987) removed *Rugathodes* Archer 1950 from *Theridion,* and Platnick (1997), following Wunderlich's and Archer's (1950) views, formally

transferred from *Theridion* to *Rugathodes* two species included in our current study, *Rugathodes sexpunctatus* (Emerton 1882) and *Rugathodes aurantius* (Emerton 1915). *Wamba crispulus* (Simon 1895), another species in our study and one considered by Levi (1963) to belong to *Theridion,* was transferred to *Wamba* by Wunderlich in 1995. The other eleven of the 14 species included in our study still remain in *Theridion,* but some of these may be removed following phylogenetic analysis (I. Agnarsson & M. Arnedo pers. comm.). Both morphological (Levi 1957) and molecular (M. Arnedo pers. comm.) evidence indicate that *Theridion frondeum* Hentz 1850 and *Theridion albidum* Banks 1895 are sister species and that *R. sexpunctatus* and *R. aurantius* are also sister species. Morphological evidence indicates that *Theridion cheimatos* Gertsch and Archer 1942 will eventually be

transferred to *Rugathodes* (I. Agnarsson pers. comm.).

The need to learn more about habitat preferences, life histories, and other facets of species' natural histories before being able to answer important questions about the structure and dynamics of communities has been emphasized by many (e.g., Duffy 1978; Strong et al. 1984; Wilson 1992; Polis et al. 1996). Our goal is to begin providing these kinds of information for North American species of *Theridion, Rugathodes,* and *Wamba,* thereby making them more accessible to ecologists and other evolutionary biologists. The Great Smoky Mountains National Park Biosphere Reserve (GSMNP), due partly to its wide elevation range (275–2013 m), large size (207,000 ha), and low temperate latitude (35°35′N, in the southern Appalachian Mountains), comprises a rich mosaic of biotic communities appropriate for pursuing this goal. By distributing a systematic sampling effort among the major habitats of this park, we have expanded our knowledge of the habitat distribution patterns of these 14 related theridiid species, completed the first life history analyses for three of them, and added knowledge about their reproductive biology.

We also hope that such knowledge will begin to help us evaluate this group's potential as an indicator assemblage (a group of species that can be used to monitor and predict changes or species richness in biotic communities). The search for such indicator groups is an important focus of some ecologists, conservation biologists, and environmental monitoring agencies (Thomas 1972; Kremen et al. 1993; Colwell & Coddington 1994; Russell et al. 1995; Norris 1999). An ideal indicator group should be easily sampled, abundant, diverse, geographically widespread, sensitive to environmental change, and important to community dynamics (Noss 1990; Kremen et al. 1993). Since spider taxa appear to meet these criteria (e. g., Uetz 1979; Coyle 1981; Bracher & Bider 1982; Christenson et al. 1990; Riechert & Bishop 1990; Coddington & Levi 1991; Carter & Rypstra 1995), they deserve to be included in the search for indicator taxa.

METHODS

Habitat distribution.—A team of four collectors used a modified Coddington sampling protocol (Coddington et al. 1996) to obtain the

668 one-hour ground (235), aerial (172), beat (206), and sweep (55) samples used in this project. Ground collection involved searching mostly on hands and knees, exploring leaf litter, logs, rocks, and plant surfaces below knee level (ca. 0–49 cm above ground). Aerial sampling involved searching leaves, branches, tree trunks, and spaces in between, from knee height up to maximum overhead arm's reach (ca. 50–220 cm above ground). Beating consisted of striking vegetation with a 1 m long stick and catching the falling spiders on a 0.5 m² canvas sheet held horizontally below the vegetation. Hands and aspirators were used to collect the spiders into 80% ethanol. One sample unit equaled 1 hour of uninterrupted effort with one of these three methods during which the collector attempted to collect every spider encountered. During each hour the team as a whole used all three methods in the same area. In the non-forest communities (grass bald, mountain wetland, and native grassland sites) 1-hour sweep sampling was substituted for aerial and/or beating methods (see Appendix); sturdy sweep nets with 38 cm diameter hoops were used and the number of sweeps per hour (175–400, mean and SD = 268 ± 47.7) depended primarily on vegetation structure and spider abundance.

Two sets of samples (one in the spring and one in late summer) were collected from 17 focal sites, each site representing one of the 16 major habitat (community) types found in the GSMNP. Habitat type, locality data, collecting dates, and sample sizes for each method at each site are given in the Appendix. At each site (except for the high grass bald, Table Mountain pine, and Indian Creek wetland sites) equal or nearly equal numbers of samples were collected with each of the methods employed. Two of the sites (low grass bald and heath bald) were sampled in 1995. The others were sampled in 1996. All adult and juvenile *Theridion, Rugathodes,* and *Wamba* specimens were sorted from each sample and identified to species. The pigment patterns are distinctive for each species in all but the first instar. The most similar species, *T. frondeum* and *T. albidum,* differ in the form of the longitudinal median marks on the carapace; *T. frondeum* has two lines or a broad band and *T. albidum* has one line. Voucher specimens for each species have been deposited in the

National Museum of Natural History, Smithsonian Institution.

The relative abundance (mean number of individuals per 1-hour sample) of each species was computed for each of the 17 sites. This index of abundance does not show the often wide variation in number of individuals among 1-hr samples at each site. This variation is due largely to the fact that each method samples only a subset of microhabitats, to spatial environmental variation within each site, and to seasonal changes in spider abundance correlated with species' phenologies. Shannon diversity and Pielou's evenness indices were used to measure the diversity of these theridiid species at each site (Magurran 1988).

Life history.—For the three most common species (*R. aurantius, R. sexpunctatus,* and *T. frondeum*) tibia I length (ITL) was measured along its dorsal surface in every specimen collected at a site where the species was common. Toft (1976) demonstrated that ITL distinguishes spider instars more clearly than does either the length or width of the carapace. Measurements were performed with a Wild M-5 stereomicroscope at $50\times$ magnification and are accurate to ±0.0185 mm. StatView 4.5 (Abacus Concepts) was used to generate ITL frequency distribution histograms for these samples. From these histograms it was possible to determine instar number. Instars were also distinguished by the distinctive widths of the palpal tarsi of penultimate and, for *R. aurantius* and *R. sexpunctatus,* antepenultimate males. The maximum width of the palpal tarsus in dorsal view (PTW) was measured at $100\times$ magnification (accurate to ±0.00925 mm) for instar III specimens of *R. aurantius* to confirm this. Phenology and generation time were determined by examining the relationship between instar distribution and collecting date. These life history analyses were based on ITL measurements of 375 *R. aurantius,* 139 *R. sexpunctatus,* and 843 *T. frondeum* individuals (see Figs. 3, 5 and 6 for the sites and dates represented by these samples). The pattern of early postembryonic development was determined by examining (at $24–100\times$ magnification) the spiderlings and shed exuviae in eleven *R. aurantius* and four *T. frondeum* egg sacs containing spiderlings. One field collected antepenultimate male and an antepenultimate female of *R. aurantius* were reared to adulthood.

Other observations.—The vertical microhabitat distribution for each species was analyzed by computing its relative abundance in aerial (above knee level) vs. ground (below knee level) samples. Beat and sweep samples were not used because each of these methods sampled spiders both above and below knee-level. The Mann Whitney U test was used to see if the relative abundance values for ground and aerial samples were significantly different (at $P < 0.05$). Field notes, sketches, measurements, and close-up photos of webs and spiders were used to characterize web structure and spider behavior. Prey items were collected from webs in the field. Egg diameters were measured with a Wild M-5 stereomicroscope at $50\times$ magnification with an accuracy of ±0.0185 mm. Clutch sizes were determined by counting the number of eggs and spiderlings in each field-collected egg sac. An unpaired *t*-test was used to determine if clutch size and body size differed significantly between early and late summer samples of *R. aurantius* and if egg and body sizes of *R. aurantius* differed significantly from those of *T. frondeum.* Several live specimens (predominantly adult females, most with egg sacs) of *R. aurantius* and *T. frondeum* were kept in small transparent plastic terraria for a few weeks to observe rates of brood development and behavior.

RESULTS

Habitat distribution.—Fourteen *Theridion, Rugathodes,* and *Wamba* species were found in the GSMNP. At each of the seven highest elevation sites (over 1500 m) one of these species was much more abundant than any other (Table 1, Fig. 1). *Rugathodes sexpunctatus* was common (relative abundance = 0.5–2.0) or abundant (relative abundance > 2.0) in the spruce-fir (1830 m) and spruce (1715 m) sites, *R. aurantius* was abundant in the high grass bald (1755 m) and beech gap (1645 m) sites, and *T. frondeum* was abundant in the northern hardwood (1615 m), red oak (1555 m), and low grass bald (1505 m) sites. Middle to low elevation sites (below 1400 m) tended to contain more species (2–8, mean and SD = 4.4 ± 1.6) than the high elevation sites (2–4, 2.4 ± 1.0) and to lack abundant species. Shannon diversity and Pielou eveness index values for the sets of these species at each site show this same pattern (Table 2).

Table 1.—Relative abundance of *Theridion, Rugathodes* and *Wamba* species at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park. Species arranged alphabetically by species name. The single specimen of *T. alabamense* was found in a leaf litter sample.

Habitat and elevation (in m) of focal site	Relative abundance (mean number of specimens per 1-hour sample)													
	alaba-mense	*albidum*	*aurantius*	*cheima-tos*	*crispulus*	*differens*	*flavono-tatum*	*fron-deum*	*glauces-cens*	*lyricum*	*murari-um*	*neshami-ni*	*pennsyl-vanicum*	*sexpunc-tatus*
Spruce-fir (1830)			0.13											1.71
High grass bald (1755)		0.04	5.92					0.21						0.13
Spruce (1715)			0.04											3.13
Beech gap (1645)			11.38											
Northern hardwood (1615)			0.02					1.13						0.02
Red oak (1555)								8.07		0.04				
Low grass bald (1505)					0.03			3.50				0.07		
Heath bald (1390)					0.01	0.03		3.71		0.35				0.43
Mixed oak (1115)		0.02						0.15		0.07				
Table Mountain pine (1005)					0.06	1.15		0.27		1.33				
Hemlock-hardwood cove (945)		0.12								0.21				
Hemlock (885)		0.08			0.10	0.15	0.13	0.48	0.15	0.33				0.48
Hardwood cove (740)		0.69				0.04	0.14	1.11	0.09	0.48	0.02			
Wetland (Indian Cr.) (685)	0.02	0.54		0.06			0.47			0.18			0.06	
Wetland (Meadow Br.) (535)		0.53		0.06										
Native grassland (520)		1.18		0.67			0.71	0.04		0.06			0.18	
Pine-oak (395)		0.04			0.02					0.92				
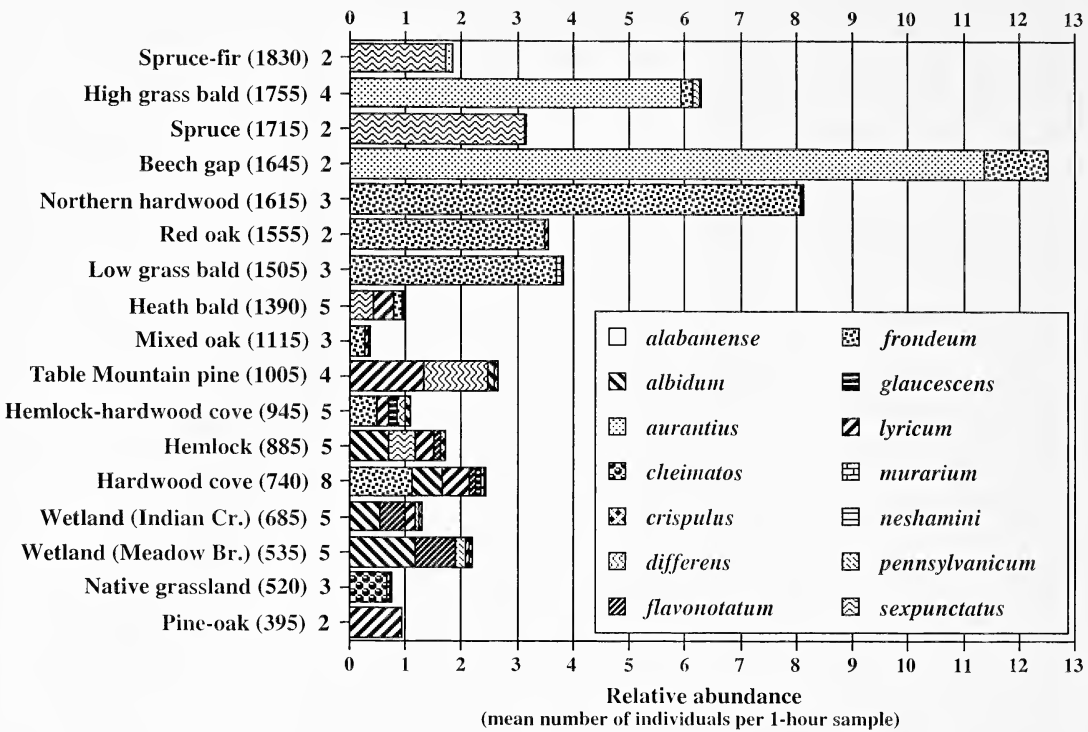
Figure 1.—Stack-bar diagram showing relative abundance of *Theridion, Rugathodes* and *Wamba* species at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park. Focal sites are listed by habitat in order from highest to lowest elevation (in m) and number of species found at that site are given after elevation.

Table 2.—Species richness and diversity values for assemblages of *Theridion, Rugathodes* and *Wamba* species at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park.

Habitat and elevation of focal site (in m)	No. of samples	Observed richness	Diversity index (Shannon)	Evenness index (Pielou)
Spruce-fir (1830)	24	2	0.25	0.36
High grass bald (1755)	24	4	0.28	0.20
Spruce (1715)	24	2	0.07	0.10
Beech gap (1645)	24	2	0.30	0.44
Northern hardwood (1615)	44	3	0.04	0.03
Red oak (1555)	48	2	0.06	0.09
Low grass bald (1505)	72	3	0.36	0.32
Heath bald (1390)	72	5	1.18	0.73
Mixed oak (1115)	45	3	0.70	0.64
Table Mountain pine (1005)	33	4	0.93	0.67
Hemlock-hardwood cove (945)	48	4	1.42	0.88
Hemlock (885)	48	5	1.40	0.87
Hardwood cove (740)	56	8	1.47	0.71
Wetland (Indian Cr.) (685)	17	5	1.28	0.80
Wetland (Meadow Br.) (535)	17	5	1.10	0.68
Native grassland (520)	24	3	0.64	0.58
Pine-oak (395)	48	2	0.11	0.16

The only middle to low elevation site with diversity and evenness values as low as those of the high elevation sites was the pine-oak site. The hardwood cove site appears to possess the greatest number of species (8). Both wetland sites had the same five species, and at each of these two sites *T. albidum* and *T. flavonotatum* were more common than the other three species and about equally abundant.

Theridion frondeum was found in more habitats (10 of 16) than any other species, and was especially abundant in the high elevation hardwood communities and the low grass bald, which is surrounded by high elevation hardwood (Table 1, Fig. 1). *Theridion albidum,* the sister species of *T. frondeum,* was found in almost as many habitats (8) but was virtually absent from high elevation habitats. Both of these species occur over a wider elevation range (1220 m) than any other species. *Rugathodes aurantius* is restricted to, and its sister species, *R. sexpunctatus,* is most abundant in, high elevation communities, but wherever one of these species is abundant or common, the other is uncommon (relative abundance < 0.5) or absent. *Theridion lyricum* Walckenaer 1841 was found in nine habitats, including a wide range of middle to low elevation communities, but appears to be most common in dry, pine-dominated, forests. Three of the less common species appear to be associated primarily with a single community type: *T. flavonotatum* Becker 1879 with wetland, *T. differens* Emerton 1882 with Table Mountain pine, and *T. cheimatos* Gertsch and Archer 1942 with native grassland. Six species (*T. alabamense* Gertsch and Archer 1942, *T. glaucescens* Becker 1879, *Wamba crispulus* (Simon 1895), *T. murarium* Emerton 1882, *T. neshamini* Levi 1957, and *T. pennsylvanicum* Emerton 1913) were uncommon wherever they occurred and, with one exception (*Wamba crispulus*), were found in only one or two habitats.

Microhabitat distribution.—Four species, *T. albidum, T. differens, T. frondeum,* and *R. sexpunctatus,* were equally common below and above knee level (Fig. 2). *Theridion cheimatos* was found only below knee level. *Rugathodes aurantius* was more common below than above knee level, but the difference is not significant ($P = 0.12$). *Theridion lyricum* was significantly more common above than
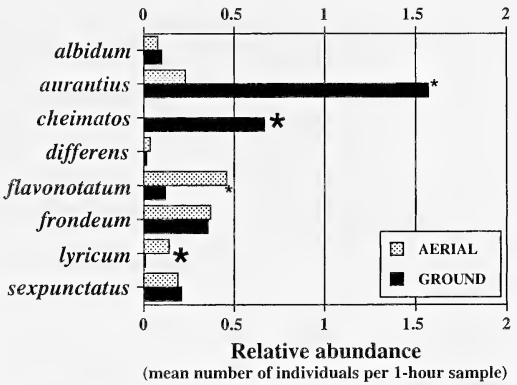
Figure 2.—Vertical microhabitat distribution of *Theridion* and *Rugathodes* species as indicated by relative abundance in aerial and ground samples from those sites where the species has been collected. Only those species found in ground and/or aerial samples at two or more sites are included. Aerial samples from 50 to 220 cm above ground; ground samples below 50 cm. Large asterisks indicate significant differences ($P < 0.05$), small asterisks differences at $0.05 > P < 0.13$.

below knee level; *T. flavonotatum* exhibits the same pattern, but the difference is not significant ($P = 0.08$). *Theridion flavonotatum* webs were common in the tops of relatively tall leafless stalks of dead herbaceous plants at both wetland sites. Nearly all *R. aurantius* webs were found on the undersides of the leaves of low herbs in clearings (grass balds, trailsides, and areas of sparse canopy in beech gap forest). *Rugathodes sexpunctatus* was collected primarily by beating low branches of young fir or ferns in spruce-fir and spruce forest. All *T. cheimatos* specimens collected at the native grassland site were found on the ground near a drainage ditch. *Theridion glaucescens* appeared only in beat samples. The single specimen of *T. alabamense* was collected in a leaf litter sample.

Life history.—There are five instars in the life cycle of *R. aurantius* (Fig. 3). Instar I, which is confined to the egg sac, lacks eyes, pigment, spigots, and visible hairs (at 100× magnification). Instar II has eyes, pigment around the eyes, functional spinnerets, and many fully developed hairs. It is also the active spiderling instar that emerges from the egg sac; this was confirmed by examining and measuring newly emerged spiderlings reared in the laboratory and by observing that instar II spiderlings inside the sac have the same ITL

Figure 3.—Size (ITL) frequency distribution histograms for five samples of *Rugathodes aurantius* from three sites. For each sample, females and individuals too young to be sexed are graphed separately from males. All five samples were pooled to generate the instar summary histograms at the bottom. Arrows in instar summary histogram mark ITL values of the penultimate instar exuvia of two specimens reared to adulthood in captivity.
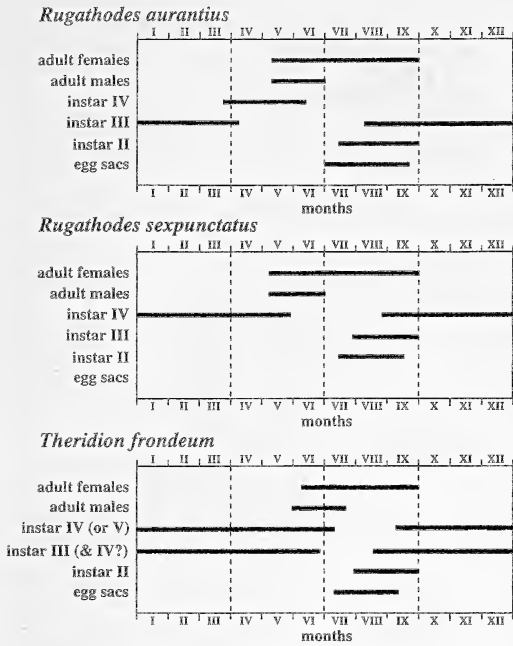
Figure 4.—Postulated phenologies for two *Rugathodes* and one *Theridion* species in the Great Smoky Mountains National Park. Based on size frequency distribution analyses and additional observations.

as the smallest solitary (post-dispersal) instar collected in the field. Instar III is the antepenultimate instar. This was confirmed by rearing an antepenultimate male and an antepenultimate female collected at Mt. Buckley to the adult instar and measuring the exuvia. The palpal tarsi of antepenultimate males were significantly ($P < 0.0001$) wider (PTW = 0.111–0.130, mean and SD = 0.117 ± 0.008, n = 15) than those of same-aged females (0.065–0.074, 0.067 ± 0.004, n = 15). Instar IV is the penultimate instar; this was confirmed by rearing the two aforementioned Mt. Buckley spiders and by finding one female of that size class at the beech gap site with an epigynum visible through her soon-to-be-molted cuticle. Instar V is the adult instar. The life cycle pattern most consistent with these data (Fig. 3) is that of one generation per year, with most individuals over-wintering in the antepenultimate instar and males and females maturing and mating in May and June (Fig. 4). This hypothesis was further supported by finding 15 individuals—all antepenultimate males and females—in leaf litter samples collected under the snow at the beech gap site on 12 February

1997. The absence of adult males from all summer and fall collections made after 27 June suggests that they die soon after mating. Many of the females collected at the beech gap site on 9 July and 15 August and at Mt. Buckley on 14 September were guarding single egg sacs. Sexual dimorphism in ITL first appears in instar III and is much greater in subsequent instars (Fig. 3). We found female-biased sex ratios (females/males) in every sample of instar III (6.0 at the beech gap on August 15 (n = 35), 1.5 at the same site on 12 February (n = 15), 6.0 at the high grass bald on 22 September (n = 57), and 2.1 at Mt. Buckley on 14 September (n = 40)).

There are five instars in the life cycle of *R. sexpunctatus* (Fig. 5). Based on observations of its sister species, *R. aurantius,* we presume that instar II of *R. sexpunctatus* is the active instar that emerges from the egg sac. The males of instars III and IV can be distinguished from each other and from females by distinctive widths of the palpal tarsi. Instar V is the adult instar. The life cycle pattern (Fig. 4) most consistent with the data is that of a single annual generation that over-winters chiefly in the penultimate instar, as indicated by the relatively large number of penultimate spiders collected in September. A collection of six individuals (four penultimate females, one penultimate male, and one instar III female) at Mt. Buckley on 25 September also supports this phenology. Males and females apparently mature and mate in May and June. Adult males are absent from late summer collections, suggesting that they die soon after mating. Some adult females persist until at least mid-September. Sexual dimorphism in ITL first appears in instar III, is much greater in the following instars, and appears to be even more pronounced in *R. sexpunctatus* than in *R. aurantius* (Fig. 5). The sex ratios (females/males) in instars III and IV of the total *R. sexpunctatus* sample are 1.6 (n = 29) and 1.1 (n = 30) respectively.

There are five or six instars in the life cycle of *T. frondeum* (Figs. 6, 7). Development in the egg sac includes the same two instars as in *R. aurantius.* Instar II spiderlings in the sac have the same ITL as the smallest solitary (post-dispersal) field-collected instar; this shows that instar II emerges from the egg sac. Only in the penultimate instar do males have distinctively wider palpal tarsi than females.
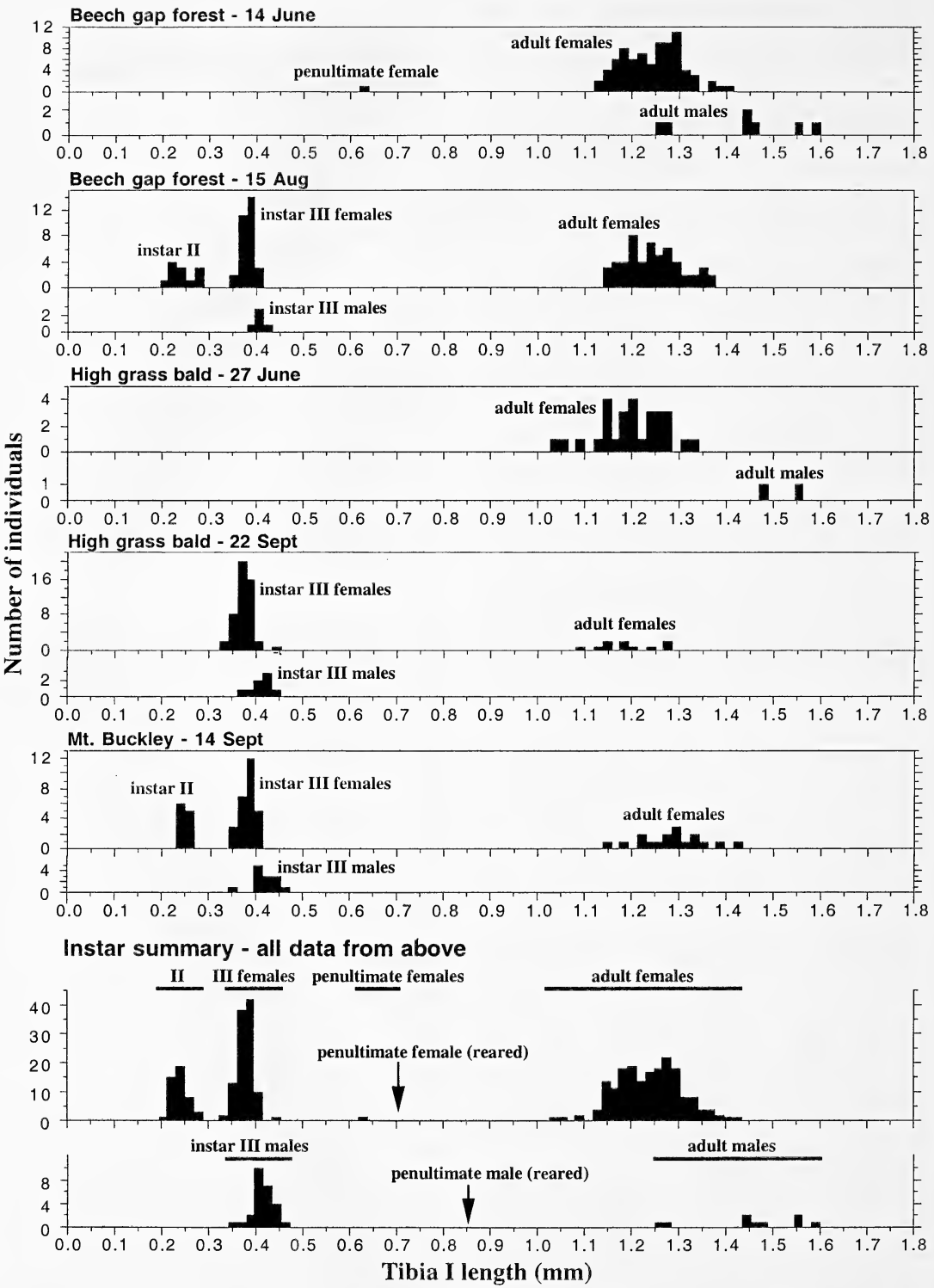
Figure 5.—Size (ITL) frequency distribution histograms for six samples of *Rugathodes sexpunctatus* from three sites. For each sample, females and individuals too young to be sexed are graphed separately from males. All six samples were pooled to generate the instar summary histograms at the bottom.
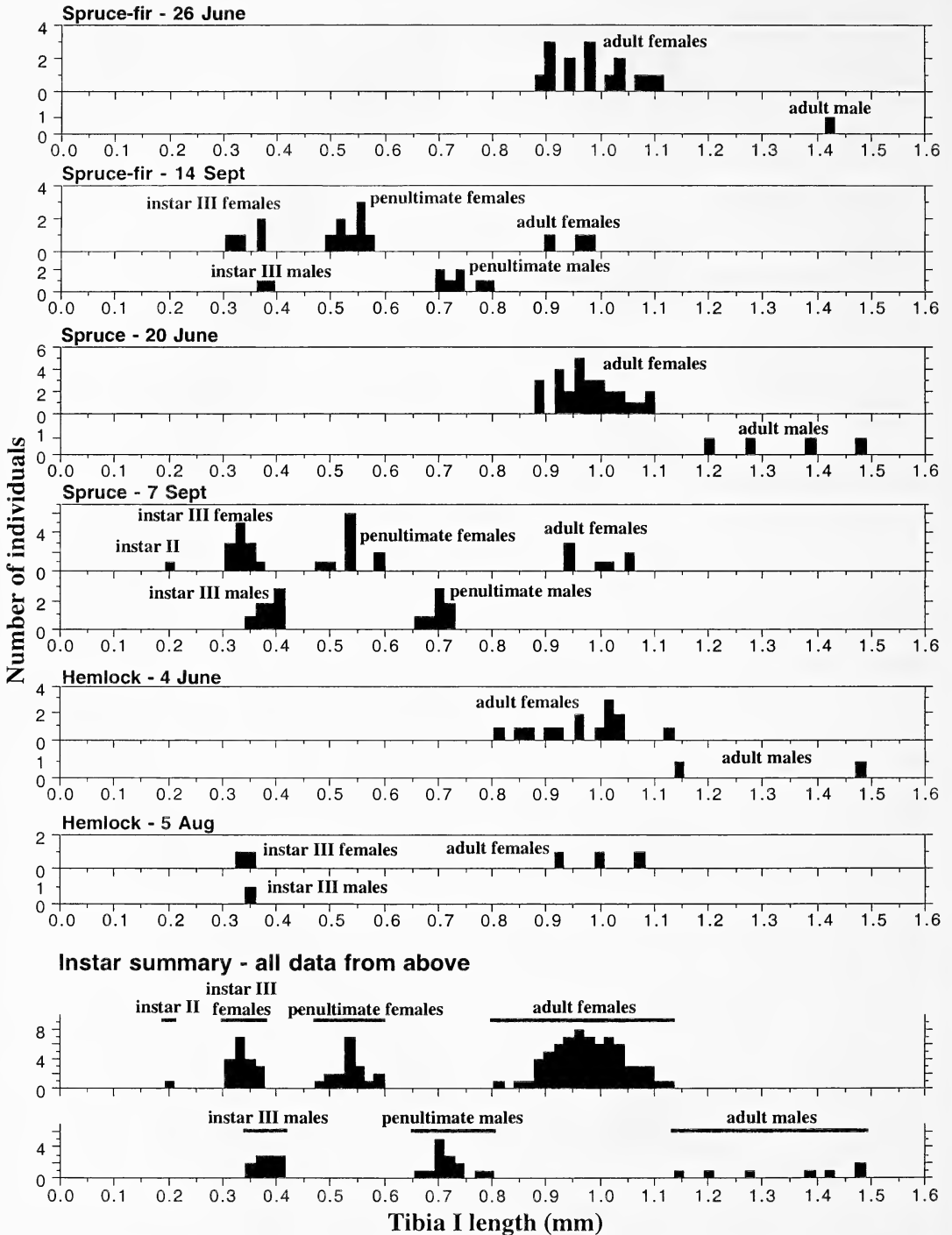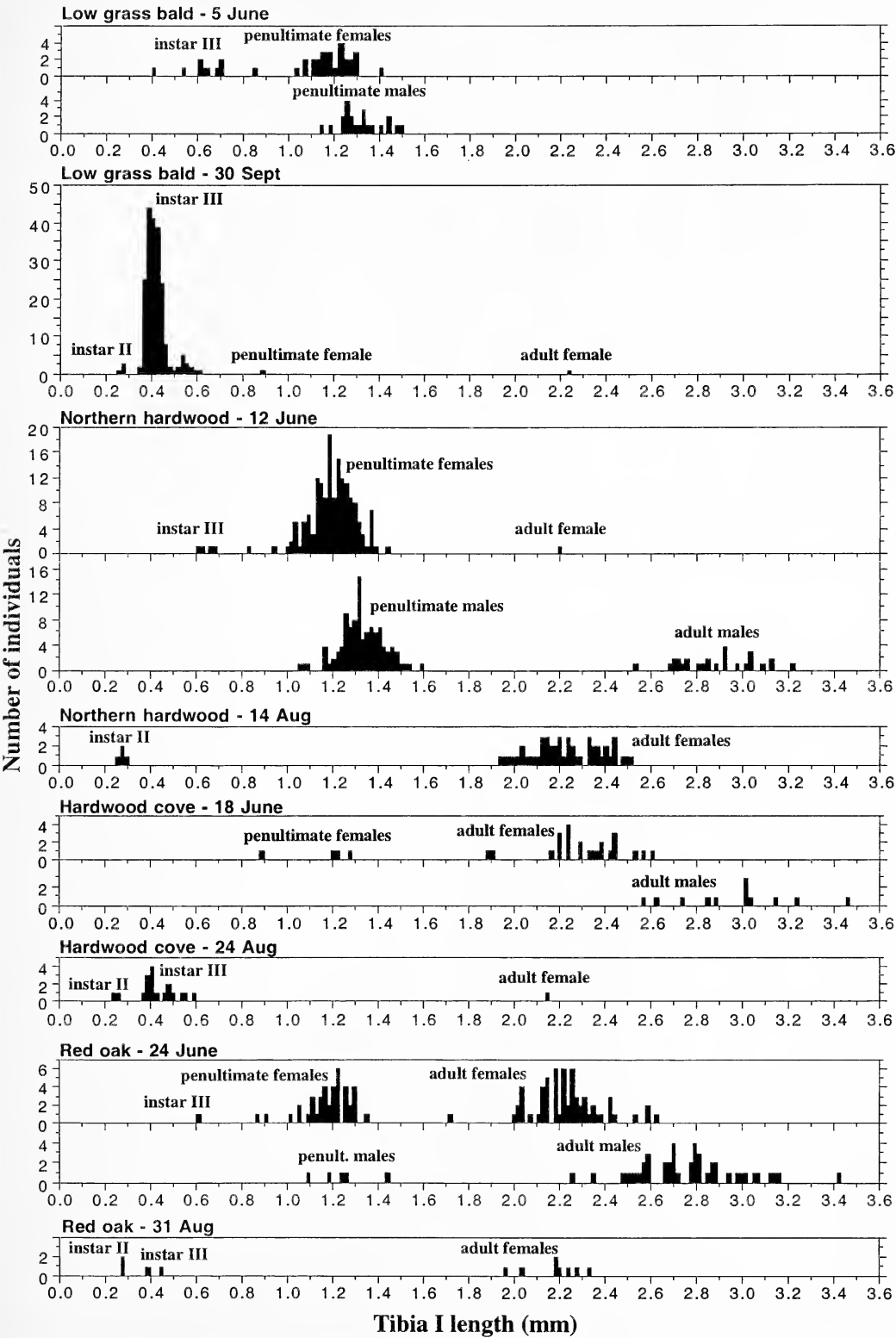
Figure 6.—Size (ITL) frequency distribution histograms for eight samples of *Theridion frondeum* from four sites. For each sample, females and individuals too young to be sexed are graphed separately from males.
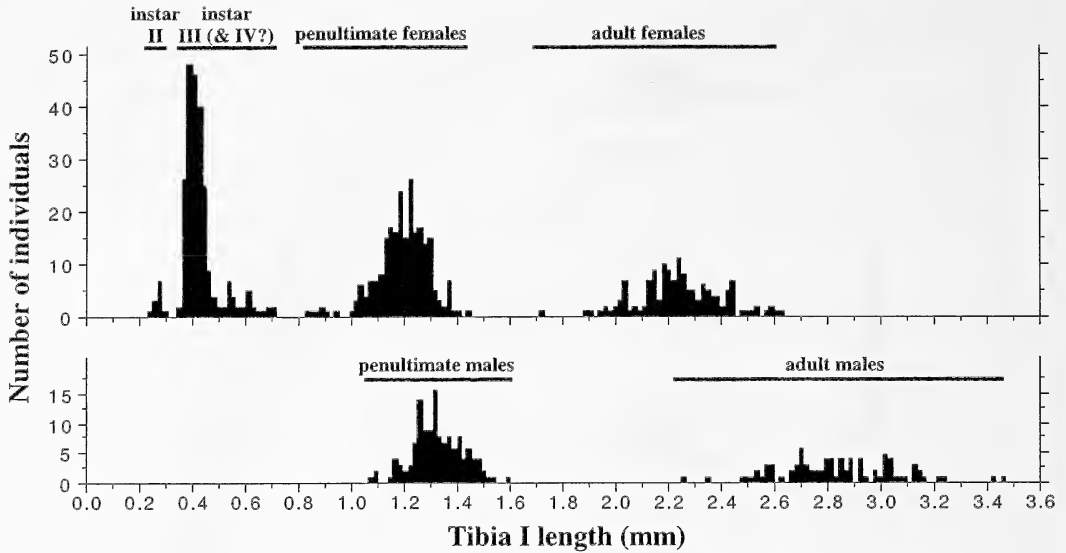
Figure 7.—Instar summary histogram for *Theridion frondeum.* Generated by pooling all data in Fig. 6.

An epigynum was visible through the soon-to-be-molted cuticle of several penultimate females. There are two lines of evidence suggesting that the size class labeled instar III in Fig. 7 may actually include instar IV individuals as well. This size class is broad and skewed strongly to the left. And the seasonal histograms (Fig. 6) show that many of the individuals that comprise the low right shoulder of this size class were collected in early June (Fig. 6), suggesting that a mid-May collection may have contained a large proportion of individuals with ITL values between 0.5 and 0.7 mm. Such a class, if present, would have to be instar IV, and would mean that at least many adults of *T. frondeum* are in their sixth instar. The life cycle pattern most consistent with the data is that of one generation per year, with over-wintering primarily in the antepenultimate instar (Fig. 4). Males and females apparently mature and mate in June and July. Since males at each site in June exhibit a higher ratio of adults to juveniles than do females, it is clear that males tend to mature before females. The absence of adult males from late summer collections suggests that they die off soon after mating. Sexual dimorphism in ITL is apparent in penultimate and adult instars. The sex ratio (females/males) in the total *T. frondeum* penultimate instar sample is 1.9 (*n* = 362) (Fig. 7).

Other natural history observations.—*Rugathodes aurantius*.—*Web placement and structure: Rugathodes aurantius* webs are virtually restricted to the herb layer. Most adult female webs were found on the broad-leafed herbs *Solidago glomerata* Michaux, *Angellica* sp., *Agertina altissima* King & Robinson var. *roenesis*, and *Aster divaricatus* L. All of these species were common at the beech gap forest site wherever tree gaps permitted the development of a rich herb layer. Most *R. aurantius* collected in the high grass bald were found in dense patches of *S. glomerata.* At Mt. Buckley (1998 m) webs were found almost exclusively in a small clearing dominated by *S. glomerata* (11 adult females and 40 juveniles were collected in a 1-hour ground sample) and were virtually absent from the adjacent spruce-fir forest (only one adult female was collected—from ferns—in 3 hours of ground collecting and beating). Adult female webs are primarily confined to the underside of a single leaf or leaflet. Roughly parallel strands of silk attached to the leaf edges bend or fold the leaf, and the bulk of the web is an asymmetrical cobweb sheltered within the resultant concavity. The spider typically rests near the center of the web on or within a few mm of the retreat leaf's ventral surface. Three types of leaf modification were observed in detail at the beech gap site on 9 July (*n* = 9 webs). The first type was characterized by strands of silk running from the tip to the base of the leaf and bending the leaf tip and adjacent edges downward and toward the leaf base, the sec-

ond by lines pulling the lateral edges of the leaf to within 5 cm of each other to form a length-wise fold, and the third by lines connecting a lateral edge fold near the base of the leaf to the tip fold, forming a cone-shaped retreat. Juvenile spiders do not appear to modify leaf shape; those collected at Mt. Buckley on 14 September were found, like adult females, on the undersides of *S. glomerata* leaves, but their webs were smaller and positioned in the natural concavity of the leaf undersurface.

Diet: Prey items found in the webs of two adult female and two instar II spiders at Mt. Buckley included three Homoptera (two green leaf hoppers [Cicadellidae] 3.5 and 3.4 mm long and one other homopteran 1.3 mm long), three small muscoid Diptera (2.1–3.5 mm long), and two other small unidentified winged insects. Beside the trail to the high grass bald site, the web of one female contained her recently emerged instar II spiderlings and the exoskeletal remains of four midges (2.2–2.5 mm long) and one small (8.5 mm long) cranefly.

Reproduction and brood care: Rugathodes aurantius females were found in nature guarding egg sacs close to the undersurface of their retreat leaf from early July to mid September. No female was observed with more than one egg sac. The spherical white egg sac is composed of a single fairly dense layer of kinky/looped threads. The diameters of 5–10 *R. aurantius* eggs in each of nine clutches (egg sacs) ranged from 0.48–0.59 mm (mean and SD = 0.54 ± 0.03 mm). Clutch sizes at two sites (beech gap forest and Mt. Buckley clearing) ranged from 3–47 (24.6 ± 13.7, n = 30). Clutch size was significantly larger (P < .0001) at the beech gap forest site on 9 July (11–47, 35.5 ± 9.7, n = 15) than on 15 August (3–23, 12.2 ± 6.2, n = 11). Clutch size of the 14 September Mt. Buckley sample was also significantly lower (14–24, 17.8 ± 4.3, n = 4, P = .003) than that of the 9 July beech gap sample. Females collected with egg sacs at the beech gap site on 9 July were significantly larger (P = .0001) (ITL = 1.18–1.39, 1.30 ± 0.05, n = 14) than those collected on 15 August (1.15–1.30, 1.22 ± 0.04, n = 11).

When disturbed, females with egg sacs typically maintained contact with the sac and often moved it. At least one of the fourth legs was used to position and move the sac, which, in a few cases, was clearly seen to be attached

to the spinnerets. The time between oviposition and emergence of instar II spiderlings from the sac was 13 days for the only brood oviposited in captivity. Spiderlings emerged from the eight field-collected egg sacs between 2 and 9 days (mean and SD = 5.9 ± 2.3) after they were collected, also suggesting that the normal period of development in the egg sac is about 2 weeks or less. Several hours before spiderling emergence, the female repeatedly and vigorously bit at the egg sac, pulling and stretching the silk to create a hole through which instar II spiderlings soon began to emerge. In the field, females were commonly found with emerged instar II spiderlings, and in one case the remains of several Diptera were present in such a web, but we saw no evidence of communal feeding. One captive female captured *Drosophila* flies and placed them near her recently emerged instar II spiderlings, which appeared to increase in size (abdominal volume) over the course of three weeks; however we never actually observed the spiderlings feeding.

Theridion frondeum.—*Retreat placement and structure:* Adult females were found inside partly folded living leaf retreats from 30 to 220 cm above ground in a great variety of plants, both herbaceous (stinging nettle, ferns, blackberries, etc.) and woody (striped maple, sugar maple, etc.). Part of the leaf is folded downward longitudinally, transversely, or diagonally. Some, for example, were folded downward sharply near the middle at one side with the opposing edges on that side fastened together with silk to make a roughly cone-shaped retreat.

Diet: A wrapped and partly consumed 5.4 mm long adult female *Pityohyphantes costatus* (Hentz 1850) spider was found in a web occupied by a 3.3 mm long *T. frondeum* female and her emerged instar II spiderlings.

Reproduction and brood care: Theridion frondeum females were found in leaf retreats with egg sacs from early July to late August. No female was observed with more than one egg sac. The spherical white egg sac is composed of a single fairly dense layer of kinky/looped threads. The diameters of ten eggs in each of two clutches ranged from 0.67 to 0.78 mm (mean and SD = 0.72 ± 0.03 mm). Clutch size ranged from 13–40 (26.8 ± 11.5, n = 5). The time from oviposition to the emergence of instar II spiderlings from the

egg sac took 13 days for the only viable brood oviposited in captivity. Two females were observed vigorously biting their egg sacs prior to spiderling emergence. In the summer spiderlings are often found with the mother in her web, suggesting that they remain there for at least a few days before dispersing.

Theridion albidum.—One female was found at the hardwood cove site on 24 August in a partly folded leaf retreat at knee level guarding an egg sac containing ten spiderlings that emerged from the sac as instar II spiderlings about 4 days later in captivity.

Theridion differens.—One female was found at the Table Mountain pine site on 6 August 1997 guarding her pale grey-brown egg sac attached to her small conical silk retreat in the junction of a leaf petiole and twig on a mountain laurel branch at about head height. She continued to cling tightly to her egg sac after being transported to the lab in a glass vial. Her entire clutch of 25 instar II spiderlings emerged from the sac by the following morning.

Theridion lyricum.—One female was collected at the hardwood cove site on 25 August with her egg sac containing 82 instar I spiderlings. The pale grey-brown sac was composed of kinky/looped strands of silk, some of which were brown, not white.

DISCUSSION

Habitat and microhabitat distribution patterns.—The differences among the 16 sampled habitats (and the great similarity of the two widely separated wetland sites) in the kinds and relative abundances of *Theridion* and *Rugathodes* species (Fig. 1) suggest that these species may be good predictors of habitat. The presence of more of these species in the habitat (hardwood cove forest) celebrated for its high plant diversity (Whittaker 1956), than in some of the habitats (spruce fir, spruce, beech gap, and pine-oak forests) characterized by relatively low plant diversity (Whittaker 1956), suggests a positive correlation between the species richness of this set of spider species and plant species richness. However, the finding of only three of these spider species in the plant-rich (175 species (Stratton & White 1982)) low grass bald and five in the plant-poor (12 species (Cain 1930)) heath bald completely negates this correlation. Evidently, the number of *Theridion* and *Rugathodes* spe-

cies present at a site is not a reliable predictor of plant species richness.

It is of interest that the species found in the greatest number of habitats and over the greatest range of elevations (*T. frondeum, T. albidum, R. sexpunctatus, T. lyricum,* and *T. differens*) all have relatively wide geographic and latidudinal ranges (Levi 1957), while some of the species found in only one or two habitats (*T. alabamense, T. cheimatos, T. neshamini,* and *T. pennsylvanicum*) have much smaller ranges (Levi 1957). This tendency for habitat specialists to occupy relatively small geographic ranges has been observed in many taxa (Stevens 1989), including species of *Tetragnatha, Neriene,* and *Araneus* spiders living in the GSMNP (Aiken & Coyle 2000; Wright & Coyle 2000; Davis & Coyle 2001).

Our observation that the sister species *T. frondeum* and *T. albidum* are often found at the same sites and that *T. frondeum* is generally more common than *T. albidum* is consistent with Levi's (1957) and Kaston's (1981) observations. The much greater abundance of *T. frondeum* at high elevation sites is consistent with the geographic ranges of the two species; T. *frondeum* is more common and widespread at higher latitudes (Levi 1957), and is therefore probably better adapted to cold climates, than is T. *albidum. Rugathodes aurantius* and *R. sexpunctatus,* another pair of sister species (Levi 1957; I. Agnarsson pers. comm.), are most common in high elevation communities—which is consistent with their basically boreal geographic ranges (Levi 1957)—but they exhibit striking habitat segregation. The distinctively different web placement substrates of the two species suggests that this segregation is based upon different microhabitat requirements. *Rugathodes aurantius* builds its webs on the undersides of broad-leaved herbs, which are rare on the heavily shaded ground of spruce-fir and spruce forests, whereas *R. sexpunctatus* typically lives on the foliage of young fir trees, which are rare or absent in the high grass bald and beech gap forest communities. The restriction of *R. aurantius* to high elevation habitats may be the result of climatic requirements, since an ample broad-leaved herb substratum is present at some of the other forest sites (especially northern hardwood) where *R. aurantius* is extremely rare or absent. Since *R. sexpunctatus* is found at some of our mid-

dle elevation sites, it seems to be less narrowly restricted to boreal climates. Our data suggest that it may be restricted to fine-needle conifers, which is consistent with Levi's (1957) observation that it is "usually found on coniferous trees." Our observations of *T. cheimatos* and *T. neshamini* are consistent with Chamberlin and Ivie's (1944) note that the former species was collected in moderately damp places on the ground and with Levi's (1957) observation that the latter species is associated with tall grass.

Life history.—Except for reports that *T. frondeum* matures in late June or July and that adult females produce eggs in July and survive through September (Emerton 1902; Comstock 1948; Kaston 1981), there are no published descriptions of the life cycles of the three species we have analyzed (*R. aurantius, R. sexpunctatus,* and *T. frondeum*). Based on our observations and those of Toft (1976) on several *Theridion* species living in a Danish beech forest, we postulate that in most *Theridion* and *Rugathodes* species the life cycle contains five or six instars, with instar II emerging from the egg sac. Like the three species we studied, four of the six *Theridion* species whose life cycles Toft resolved have annual (one-year) life cycles and overwinter in the antepenultimate or penultimate instars. The three species we studied differ from one another in two aspects of their phenologies (Fig. 4): *R. aurantius* overwinters in the antepenultimate instar; *R. sexpunctatus* overwinters in the penultimate instar; and *R. aurantius* and *R. sexpunctatus* mature a few weeks and possibly one instar earlier than does *T. frondeum.*

The female-biased sex ratios we observed in antepenultimate and penultimate instars of these three species may be artifacts of sampling error or may be real. The strongly female-biased ratios in the adult samples of all three species could be the result of the earlier maturation and/or shorter longevity of males, but the basis for bias in earlier instars is not so evident. Group living, which should favor selection of female sex-biasing mechanisms in social spiders (Aviles 1986, 1993), does not exist in these species.

Web placement and structure.—The diversity of leaf retreat architectures engineered by adult females of *R. aurantius* and *T. frondeum* is probably the result of a flexible response to variation in leaf form. We hypothesize that leaf retreat construction is an adaptation to protect the spider and her brood from rain, intense sunlight, and/or visual predators.

Diet.—The few prey items collected from *R. aurantius* webs suggest that small flying insects are a significant part of their diet. The data also show that both *R. aurantius* and *T. frondeum,* like other *Theridion* species (Bristowe 1958), can capture prey considerably larger than themselves.

Reproduction and brood care.—Given that *T. frondeum* females with egg sacs were significantly ($P < .001$) larger (mean carapace width = 1.12 mm ± 0.04; $n = 5$) than those of *R. aurantius* (0.85 ± 0.19; $n = 5$), it is not particularly surprising that the eggs in the two observed egg-stage clutches of *T. frondeum* were significantly larger than those of *R. aurantius* ($P < .001$). In the light of Marshall & Gittleman's (1994) findings that clutch size increases with body size across spider taxa, it is interesting that the observed clutch sizes of these two species did not differ. It is also noteworthy that the only clutch of *T. lyricum* we observed (carapace width of the mother = 0.96 mm) was nearly twice as large as the largest clutches of the other species.

Toft (1976) found that females of some *Theridion* species produce two or more (up to five) egg sacs over the course of the summer. He postulated that this ability to produce multiple clutches is a widespread fecundity-enhancing trait of small spiders that compensates for a relatively small number of eggs per egg sac. Two of our observations strongly suggest that *R. aurantius* females also produce multiple clutches: 1) the single annual cohort of adult females is found in nature guarding egg sacs throughout a 2.5 month period, even though the interval from oviposition to spiderling emergence from the egg sac is about 2 weeks; 2) there was a significant decrease in the beech gap forest site population's mean clutch size between 9 July and 15 August, a pattern commonly observed in multi-clutch spiders (Toft 1976; Marshall & Gittleman 1994). Nevertheless, we cannot rule out the possibility that *R. aurantius* females produce only one clutch and that the observed decrease in clutch size is the result of delayed oviposition by smaller females. This second hypothesis is consistent with the observation that

adult females in the 15 August beech gap sample had a significantly smaller mean ITL value than those of the 9 July sample.

Our observations of *R. aurantius* and *T. frondeum* indicate that females devote considerable effort to brood care. Bent-leaf retreat construction and egg sac guarding have been observed in other *Theridion* species (for example Archer (1947) and Bristowe (1958)), and Emerton (in McCook 1890) described an unidentified *Theridion* female assisting her spiderlings in exiting the egg sac with the same behaviors we observed in *R. aurantius* and *T. frondeum.* Our observations that instar II spiderlings of these two species remain with the mother in her retreat for at least a few days after emerging from the egg sac suggests the interesting possibility of nutritional parental care like that observed in some European and Central American *Theridion* species (Nielsen 1932; Bristowe 1958; Kullman 1972; and authors' personal observations in Costa Rica). We have observed no compelling evidence of such care, but the possibility deserves closer scrutiny.

ACKNOWLEDGMENTS

LITERATURE CITED

Aiken, M. & F.A. Coyle. 2000. Habitat distribution, life history and behavior of *Tetragnatha* spider species in the Great Smoky Mountains National Park. Journal of Arachnology, 28:97–106.

Archer, A.F. 1947. The Theridiidae or comb-footed spiders of Alabama. State Geological and Natural History Survey of Alabama. Museum Paper 22.

Archer, A.F. 1950. A study of theridiid and mimetid spiders with descriptions of new genera and species. Museum Papers of the Alabama Museum of Natural History, 30:1–40.

Aviles, L. 1986. Sex-ratio bias and possible group selection in the social spider *Anelosimus eximius.* American Naturalist 128(1):1–12.

Aviles, L. 1993. Interdemic selection and the sex ratio:a social spider perspective. American Naturalist 142(2):320–245.

Bracher, G.A. & J.R. Bider. 1982. Changes in terrestrial animal activity of a forest community after an application of aminocarb (Matacil). Canadian Journal of Zoology 60:1981–1998.

Bristowe, W.S. 1958. The World of Spiders. Collins, London. 304 pp.

Cain, S.A. 1930. An ecological study of the heath balds of the Great Smoky Mountains. Butler University Botanical Studies 1:177–208.

Carter, P.E. & A.L. Rypstra. 1995. Top-down effects in soybean agroecosystems: spider density affects herbivore damage. Oikos 72:433–439.

Chamberlin, R.V. & W. Ivie. 1944. Spiders of the Georgia region of North America. Bulletin of the University of Utah 35(9):1–267.

Christenson, T.E., J. Cohn, & M.J. Pokora. 1990. Spiders as environmental monitors of heavy metals. The Toxicologist 10:249.

Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). Annual Reviews of Ecology and Systematics 22:565–592.

Coddington, J.A., L.H. Young, & F.A. Coyle. 1996. Estimating spider species richness in a southern Appalachian cove hardwood forest. Journal of Arachnology 24:111–128.

Colwell, R.K. & J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London B 345:101–118.

Comstock, J.H. 1948. The Spider Book. Cornell University Press, Ithaca, New York. 729 pp.

Coyle, F.A. 1981. Effects of clearcutting on the spider community of a southern Appalachian forest. Journal of Arachnology 9:285–298.

Davis, M.J. & F.A. Coyle. 2001. Habitat distribution and life history of *Araneus* spider species in the Great Smoky Mountains National Park. Bulletin of the British Arachnological Society 12(2): 49–57.

Duffy, E. 1978. Ecological strategies in spiders including some characteristics of species in pioneer and mature habitats. Symposium of the Zoological Society of London (42):109–123.

Emerton, J.H. 1902. The Common Spiders of the United States. Ginn and Company. 227 pp.

Hanggi, A., E. Stockli, & W. Nentwig. 1995. Habitats of central European spiders. Miscellanea Faunistica Helvetiae, No. 4. 459 pp.

Kaston, B.J. 1981. Spiders of Connecticut. Rev. ed. State Geological and Natural History Survey of Connecticut, Bulletin No. 70.

Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7(4): 796–808.

Kullmann, E.J. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). American Zoologist 12:419–426.

Levi, H.W. 1957. The spider genera *Enoplognatha, Theridion,* and *Paidisca* in America north of Mexico. (Araneae, Theridiidae). Bulletin of the American Museum of Natural History 112:1–123.

Levi, H.W. 1959. The spider genera *Achaearanea, Theridion* and *Sphyrotinus* from Mexico, Central America and the West Indies (Araneae, Theridiidae). Bulletin of the Museum of Comparative Zoology, 121(3):57–163.

Levi, H.W. 1963. American spiders of the genus *Theridion* (Araneae, Theridiidae). Bulletin of the Museum of Comparative Zoology 129(10):481–589.

Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey. 179 pp.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8: 118–124.

McCook, H.C. 1890. American Spiders and their Spinning Work. Vol. 2. Allen, Lane and Scott. 479 pp.

Nielsen, E. 1932. The Biology of Spiders. Levin and Munksgaard, Copenhagen. 248 pp.

Norris, K.C. 1999. Quantifying change through time in spider assemblages: sampling methods, indices, and sources of error. Journal of Insect Conservation 3:1–17.

Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4(4):355–364.

Platnick, N.I. 1997. Advances in Spider Taxonomy 1992–1995. New York Entomological Society, New York. 976 pp.

Polis, G.A., R.D. Holt, B.A. Menge, and K.O. Winemiller. 1996. Time, space, and life history: influences on food webs. Pp. 435–461, *In* Food Webs: Integration of Patterns and Dynamics. (G.A. Polis & K.O. Winemiller, eds.). Chapman & Hall.

Riechert, S.E. & L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology 71:1441–1450.

Roberts, M.J. 1995. Spiders of Britain and Northern Europe. Harper Collins, London. 383 pp.

Russell, G.J., J.M. Diamond, S.L. Pimm, & T.M. Reed. 1995. A century of turnover: community dynamics at three timescales. Journal of Animal Ecology 64:628–641.

Stratton, D.A. & P.S. White. 1982. Grassy balds of Great Smoky Mountains National Park: Vascular plant floristics, rare plant distributions, and an assessment of the floristic data base. Research/ Resource Management Report SER-58, National Park Service, Natural Science Research Division, Atlanta, Georgia.

Stevens, G.C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. American Naturalist 133(2):240–256.

Strong, D.R., D. Simberloff, L.G. Abele & A.B. Thistle (eds.). 1984. Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton, New Jersey.

Thomas, W.A. (ed.). 1972. Indicators of Environmental Quality. Plenum Press.

Toft, S. 1976. Life-histories of spiders in a Danish beech wood. Natura Jutlandica 19:5–40.

Uetz, G.W. 1979. The influence in variation in litter habitats on spider communities. Oecologia 40: 20–42.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26(1):1–80.

Wilson, E.O. 1992. The Diversity of Life. Harvard University Press, Cambridge, Massachusetts. 424 pp.

Wright, R.L. & F.A. Coyle. 2000. Habitat distribution, life history and behaviour of *Neriene* species in the Great smoky Mountains national Park (Araneae, Linyphiidae). Bulletin of the British Arachnological Society 11(7):293–304.

Wunderlich, J. 1987. Die Spinnen der Kanarischen Inseln und Madeiras: Adaptive Radiation, Biogeographie, Revisionen und Neubeschreibungen. Triops Verlag, Langen, Germany.

Wunderlich, J. 1995. Revision und Neubeschreibung einiger Gattungen der Familie Theridiidae aus der Nearktis und Neotropis (Arachnida: Araneae). Beitrag Araneologie 4:609–615.

APPENDIX

Habitat type, locality data (with UTM coordinates), collecting dates, and sample sizes are given for each of the 17 focal sites (listed in order from highest to lowest elevation) and one accessory site. For focal sites, the number of ground, aerial, beat, and sweep samples are given in parentheses after total number of 1-hr samples. Whittaker (1956) provides descriptions of the vegetation of most of these habitats. A bald is a natural treeless community on a well-drained high elevation site below the climatic tree-line. A beech gap forest is an orchard-like forest dominated by small gray beech trees (*Fagus grandifolia*) and is typically located on a

south-facing slope in a high mountain gap. Hardwood cove forests are found in sheltered middle elevation sites and are characterized by a high species diversity of large trees and understory plants.

Focal sites.—*Spruce-fir forest:* North Carolina: Swain County, 0.5 km SW Mt. Collins, N&S sides of Appalachian Trail, E2755, N39403, 1815–1845 m elev., 26 June and 14 Sept. 1996, 24 (8-8-8-0).

High grass bald: North Carolina: Swain County, Andrews Bald, E2738, N39354, 1755 m elev., 27 June and 22 Sept. 1996, 24 (10-0-4-10).

Spruce forest: North Carolina: Swain County, just SW junction of Noland Divide Trail and road to pumping station, E2755, N39382, 1715 m elev., 20 June and 7 Sept. 1996, 24 (8-8-8-0).

Beech gap forest: North Carolina: Swain County, in hog exclosure below Appalachian Trail at 350 m E Road Prong Trailhead, E2786, N39433, 1645 m elev., 14 June and 15 Aug. 1996, 24 (8-8-8-0).

Northern hardwood forest: North Carolina: Haywood County, Cataloochee Divide just above Hemphill Bald Trail at 200 m E Garrett's Gap, E3055, N39359, 1615 m elev., 12&15 June and 14 Aug. 1996, 44 (15-15-14-0).

Red oak forest: North Carolina: Swain County, Roundtop Knob, E of Noland Divide Trail about 2 mi SE Clingman's Dome Road, E2770, N39364, 1555 m elev., 24 June and 31 Aug. 1996, 48 (16-16-16-0).

Low grass bald: North Carolina: Swain County, Gregory Bald, E2401, N39343, 1505 m elev., 3–5 June and 29–30 Sept. 1995, 72 (24-0-24-24-24).

Heath bald: Tennessee: Sevier County, Inspiration Point on Alum Cave Trail, E2789, N39461, 1390 m elev., 25–26 May and 23–24 Sept. 1995, 72 (24-24-24-0).

Mixed oak forest: Tennessee: Sevier County, E, S, & W slopes of Chinquapin Knob, E2639, N39512, 1083–1144 m elev., 13 June and 13 Aug. 1996, 45 (15-14-16-0).

Table Mountain pine forest: Tennessee: Sevier County, about 200 m N of route 441 loop NW of Chimneys picnic area, E2738, N39471, 976–1037 m elev., 6 June and 6 Aug. 1996, 33 (13-8-12-0).

Hemlock-hardwood cove forest: Tennessee: Sevier County, N&E Grotto Falls Trailhead at Roaring Fork Motor Trail, P. White veg. plot, E2772, N39512, 945 m elev., 22 May and 30 July and 1 Aug. 1996, 48 (16-16-16-0).

Hemlock forest: North Carolina: Haywood County, Cataloochee, 150 m S mouth of Palmer Branch at Caldwell Fork, E3107, N39436, 854–915 m elev., 4 June and 5 Aug. 1996, 48 (17-14-17-0).

Hardwood cove forest: Tennessee: Sevier County, along Porter's Creek Trail at 200 paces above bridge over Porter's Creek, E2830, N39508, 740 m elev., 18–19 June and 24–25 Aug. 1996, 56 (19-18-19-0).

Wetland (Indian Cr.): North Carolina: Swain County, marsh between Indian Creek Trail and Indian Creek at 2 mi. NE of junction with Deep Creek Trail, E2817, N39296, 685 m elev., 27 May and 16 Aug. 1996, 17 (7-3-4-3).

Wetland (Meadow Br.): Tennessee: Blount County, marsh along Meadow Branch at 0.5 km ENE of Dosey Gap, E2527, N39470, 535 m elev., 23 May and 1 Aug. 1996, 17 (7-4-0-6).

Native grassland: Tennessee: Blount County, Cades Cove, S side Abrams Creek about 0.3 mi. upstream from Cades Cove Loop Road bridge, E2426, N39423, 520 m elev., 5 June and 8 Aug. 1996, 24 (12-0-0-12).

Pine-oak forest: Tennessee: Blount County, 300 m N of junction of Tabcat Creek and Maynard Creek, E2301, N39347, 395 m elev., 28–29 May and 2 Aug. 1996, 48 (16-16-16-0).

Accessory site.—Tennessee: Sevier County, small clearing near top of Mt. Buckley and adjacent area of young fir on N slope near top of Mt. Buckley, E2720, N39380, 1980–2000 m elev., 14 Sept. 1996.

EVIDENCE FOR KIN-STRUCTURED GROUP FOUNDING AND LIMITED JUVENILE DISPERSAL IN THE SUB-SOCIAL SPIDER *STEGODYPHUS LINEATUS* (ARANEAE, ERESIDAE)

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ABSTRACT.   In sub-social spiders, restricted dispersal of young (i.e., natal philopatry) and the potential for inbreeding could contribute to within-population subdivision, thus resulting in a population structure similar to that found in social congeners. In this context, we analyzed the origin and mode of individual distribution patterns and their contribution to within-population structure in juveniles of the sub-social spider *Stegodyphus lineatus*. We investigated the distribution of juveniles for four months after leaving the maternal nest using allozyme genetic markers. We found that isolated groups of juveniles consisted predominantly of siblings, whereas larger aggregations of individuals showed mixing of different juvenile sibling groups. However, even within such aggregations, sibling groups could be identified. Within the population at large, a heterozygote deficit and an uneven distribution of alleles were found. This was caused by limited movement of juveniles and males away from the natal site. Thus, the within-population (intrademic) structure could be partitioned into two components, resulting from kin-groups and population subdivision into demes. We compare this type of population structure with that found in non-social and social species, and discuss whether it provides conditions that could favor the evolution of sociality.

Keywords: Dispersal, sibling groups, allozymes, relatedness, group founding, intrademic structure.

Species of the genus *Stegodyphus* Simon 1873 (Eresidae) experience extended maternal care, in which spiderlings continue to be fed beyond their first instars and remain together after the mother's death (Schneider 1995). There are three social species (non-territorial permanently social, *sensu* Aviles 1997) in the genus. The widespread occurrence of extended maternal care and juvenile cohabitation in the sub-social congeners suggests that permanent sociality evolved in species that were preconditioned for a prolonged phase of tolerance. This has been termed the sub-social route to sociality (Buskirk 1981). Other eresids (e.g., *Eresus* Walckenaer, 1805, *Seothyra* Purcell 1903) exhibit sub-social behavior (Kullmann & Zimmermann 1975; Y. Lubin personal observation).

High population turnover, inbreeding in closed colonies and colony founding by one or a few related females are demographic characteristics typically associated with sociality in spiders (Riechert & Roeloffs 1993; Avilés 1997). Such populations may have low levels of genetic variation overall, and in particular, individuals within groups will be genetically similar. The spatial distribution of genetic variation within a population is important, because the evolution of social traits may depend on the degree of genetic similarity among interacting individuals.

Sub-social species examined so far differ from social species in having greater genetic variability, no permanent group living, and less population structuring (Johannesen et al. 1998; Johannesen & Lubin 1999). The eresid *Stegodyphus lineatus* Latreille 1817, is considered sub-social. After a phase of living communally in the maternal nest, young *S. lineatus* disperse and settle singly. Spiders live one year, and their nests are often found in clusters separated by large distances of similar, but uninhabited habitat (Lubin et al. 1998). Dispersing young initially settle in the vicinity of the maternal web (Lubin et al. 1998) but nest relocation is not uncommon (Ward & Lubin 1993). Lubin et al. (1998) suggested that limited movement of young during dispersal and their preference for certain species of shrubs results in clumped distributions. Using

genetic markers, Johannesen & Lubin (1999) showed that *S. lineatus* form relatively stable clusters in trees and that in such clusters, adult spiders experience limited dispersal. Furthermore, these groups showed evidence of being established by single females, a pattern similar to that found in social species. However, such stable environments may be atypical sites for this species, and data on juvenile movements in more typical habitats following the initial natal dispersal phase are still lacking.

The aim of the present study was to investigate juvenile dispersal of *S. lineatus* to explain the origin and amount of within-population genetic variance and the processes that produce this variance. We investigated the distribution of juveniles 4 mo after dispersal from the maternal nest. We examined whether clusters consisted of sibling groups, and if these remained separated or if they mixed with juveniles of other clusters. Finally, we tested for the occurrence of random mating at the population level. On the basis of a previous study (Johannesen & Lubin 1999) we predicted that clusters are predominately kingroups. In contrast to the previous study, the present study analyzes a population in a wadi (dry riverbed), which is an unstable environment that is subject to occasional flooding and frequent disturbance from grazing. We ask if a stable environment is required to generate structuring within the population or if intrademic structure is an intrinsic part of the life history of *S. lineatus* in both stable and unstable environments.

METHODS

Juvenile spiders were collected from several clusters in a small wadi near Sede Boker in the Negev Desert, Israel (Fig. 1) on 25–26 October, 1998, about 4 mo after they left the maternal nest. A juvenile cluster was subjectively defined: either according to a clustered location in a specific plant or if the cluster was near to an old maternal nest showing signs of reproduction (remains of the consumed mother, exuviae of spiderlings). For every cluster, the number of occupied and unoccupied juvenile nests was noted. Two groups, 24A and 24B, were not discretely clustered but consisted of several single nests radiating from the bush-cluster of group 23 (Fig. 1). More than 200 juvenile nests were located: 79 webs were occupied by *S. lineatus,* four by another species, and 65 webs were empty. The re-

maining webs were not checked. The 79 juvenile spiders belonged to sixteen clusters. Thirteen of these clusters consisted of three or more individuals.

The population and family structure was investigated by means of genetic similarity estimates using enzyme electrophoresis. Electrophoresis staining procedures followed Johannesen & Lubin (1999). The enzymes *Aat-1, Pep-A* and *Adh* were omitted from the analysis because they did not stain or stained too weakly to be interpreted in all juveniles. These three enzymes stained weakly in adult animals. To improve the resolution of *esterase* alleles, the enzyme was run in Tris-Maleate pH = 7.8 instead of Tris-Maleate pH = 7.0.

To help investigate for an unequal distribution of alleles within the wadi, it was divided into an upper and lower half. Each wadi-half comprised about half the individuals. Random mating (Hardy-Weinberg proportions) within the total wadi population and within the upper and lower wadi, respectively, was tested by the Louis & Dempster (1987) exact test using the program GENEPOP (Raymond & Rousset 1995). Genotypic linkage disequilibria were estimated according to Weir (1991). Allele frequency differences between upper and lower wadi were tested applying a RxC—test (GENEPOP) (Fig. 1). Estimates of genetic differentiation among spider groups were obtained by the *F*-statistic estimators of Weir & Cockerham (1984), using the program Biosys (Swofford & Selander 1989). Standard deviations were obtained by jackknifing over loci. *F*-statistics assume that populations (or groups) are defined as breeding units, i.e., the individuals in a group originated from random matings of the previous generation. However, if a cluster consists primarily of siblings, the random mating assumption is violated (Chesser 1991), because by having the same parents, genes of siblings are correlated. Thus, within-population structure may be confounded owing to sampling both sibling groups and breeding units (multi-parental groups). This may lead to a population subdivision estimate based on variance between families, and not actual population subdivision.

To distinguish between genetic structure caused by breeding units and that caused by sibling groups, we used the approach outlined in Johannesen & Lubin (1999), combining a test for group relatedness and heterozygote ex-
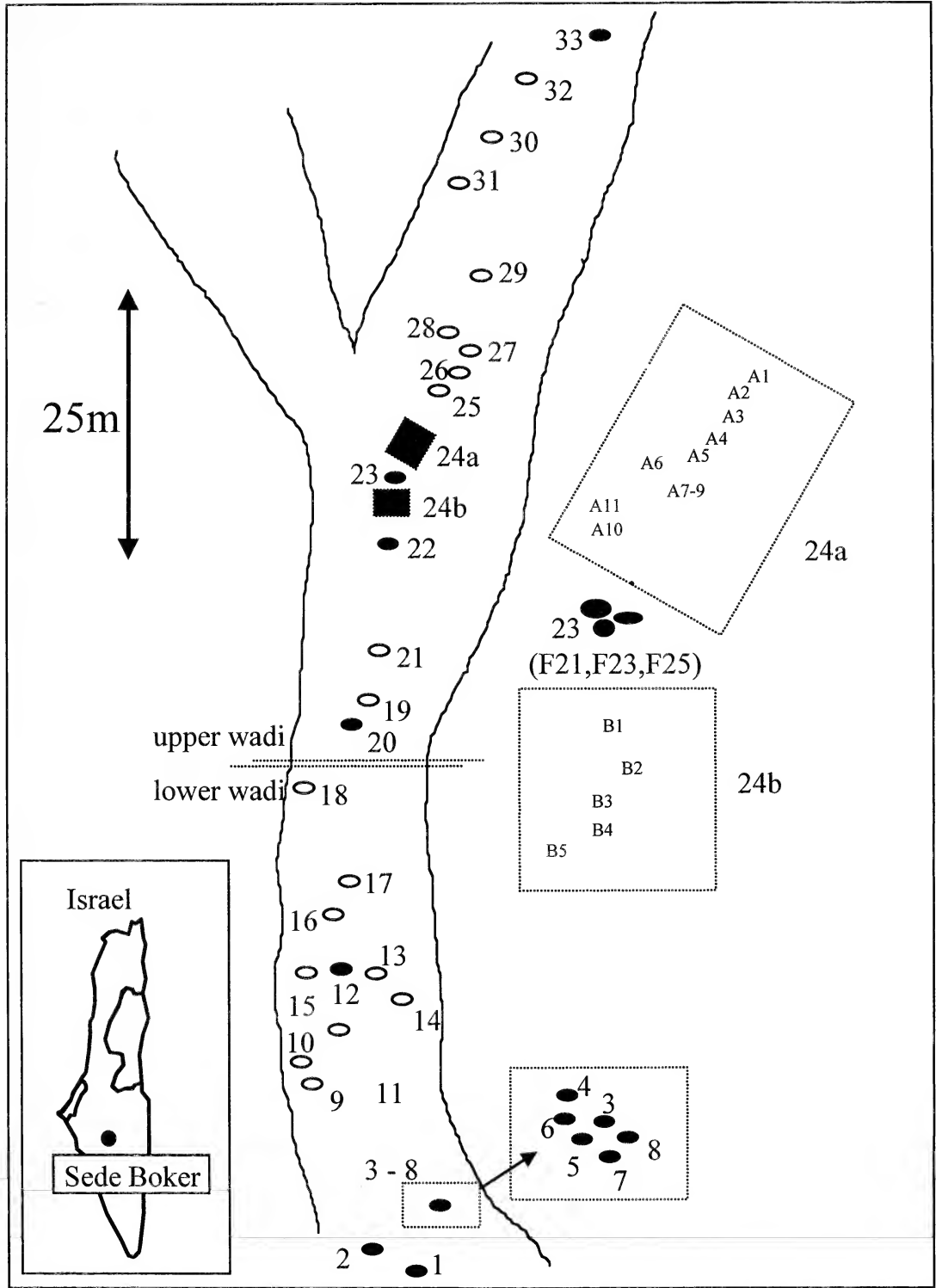
Figure 1.—Sampling location and positions of juvenile *Stegodyphus lineatus* in a wadi near Sede Boker, Israel. Filled circles represent sampled clusters.

cess. The test provides an indication of whether the relatedness of individuals in specific clusters is caused primarily by population subdivision (Wahlund effects) or by sibling relationships. In a two-allelic full-sibling group the average heterozygote excess due to the sibling effect is 7/6 pq (Rasmussen 1979). If individuals of a cluster are related, $R_{group} > 0$, and have an inbreeding index, $F_{group} < 0$, then this indicates a group of predominantly siblings. In a structured population, where the population inbreeding index $F_{IT} > 0$, if $R_{group} > 0$ and $F_{group} = 0$, then this may indicate that a cluster consists of offspring from several parents; here the positive value of R is a consequence of subdivision of the population (the Wahlund effect). It should be noted, however, that this test is a crude measure when dealing with only one or two polymorphic loci. If only one polymorphic locus is present and parents of a full-sibling group carried alternative alleles, then $F_{group} \approx 0$. F_{group} values were tested for significance using permutation tests (see Johannesen & Lubin 1999). The population-wide Wahlund effect (measured here as F_{IT}) is little affected by the sibling effect if more than four sibling groups are sampled (Rasmussen 1979). In a random mating population consisting of family groups, F_{IT} quickly approaches zero as the number of sibling groups increases.

Relatedness of group individuals was estimated according to the method of Queller & Goodnight (1989). The population R estimate was obtained by jackknifing over clusters. Only clusters having three or more individuals were analyzed in the group comparisons. For estimates concerning the total wadi population, all sampled individuals were included in the analysis. Kinship assignment of individuals to sibling groups was performed under the primary hypothesis of individuals being full siblings (paternal relatedness pR = 0.5, maternal relatedness mR = 0.5) against the null hypothesis pR = 0 and mR = 0 using the program Kinship 1.0 (Queller & Goodnight 1989). The above hypothesis of full sibling is conservative, given that we lack information about the frequency of multiple mating in natural populations.

RESULTS

A deviation from random mating (Hardy-Weinberg proportions) was found within the wadi-population, $P < 0.001$. *Pep-B1*, *Est* and *Idh* experienced a deficit of heterozygotes, whereas the two remaining high- polymorphism loci *Ak* and *Sorbdh* and the two low-polymorphism loci *Ldh1* and *Fum* did not. All rare alleles were found only as heterozygotes. Furthermore, significant deviations from Hardy-Weinberg proportions were found within both sections of the wadi (lower half $P < 0.05$, upper half $P < 0.01$). Significant differences in allele distributions was found between the upper and lower half of the wadi population ($P < 0.001$), e.g., the *Est* alleles *2* and *6* were found only in the lower half, whereas the *Ldh* allele *87* and *Fum* allele *124* were found only in the upper half. In the total wadi sample, genetic linkage disequilibrium was observed in 8 out of 21 pair-wise locus comparisons (38%). Genotype distributions are given in the Appendix.

An average group relatedness of $R = 0.25 \pm 0.12$ was observed. The relatedness estimate for single clusters ranged between -0.21 and 0.82 (Table 1). The relatively large standard deviation indicated that some groups consisted of individuals differing in their genetic background. This was confirmed by the F_{group} estimators (Table 1), where F_{group} ranged between -0.58 and 0.41. Out of the 13 examined clusters, seven showed a heterozygote excess. Based on permutation tests, nine groups had a heterozygote excess, two of which were significant. The remaining groups exhibiting homozygote excess were part of larger clusters. The finding is corroborated by the F-statistics, $F_{IT} = 0.150 \pm 0.067$; $F_{IS} = -0.070 \pm 0.073$; $F_{ST} = 0.209 \pm 0.086$, which showed that both kin (negative F_{IS}) and Wahlund effects (positive F_{IT}) enhance F_{ST}, which is the differentiation among groups (Table 1).

Kinship-analyses were performed within four groupings: clusters 3–8, cluster 12, aggregated clusters 24A, 24B, F21, F23, F25, and cluster 33, under the assumption that individuals in these clusters were full siblings. Figure 2 (see also Appendix) illustrates the kinship assignment based on the rare non-overlapping *Ak*/*Est*/*Pep-B1* allele combinations in clusters 3–8. Individuals carrying the allelic combinations tested as full-siblings belonging to one of two sibling groups. Individuals from clusters 3–8 were regrouped into two groups consisting of the predicted full-sibling assignments based on *Ak*/*Est*/*Pep-B1* allelic distributions, and the R and F_{group} values were estimated for these groups. The in-

Table 1.—Relatedness and inbreeding index estimates for clusters of juvenile *S. Lineatus* within a wadi population. Sibling group 1 and 2 estimates are based on rearrangement of individuals from groups 3–8 into two sibling groups based on allelic distributions (see text). Significant permutation F_{group}'s ($P < 0.05$) are presented in bold.

Group estimates cluster	N	Relatedness	F_{group}	Mean permutation F_{group}	sd
1	2	—	—	—	—
2	4	−0.21	0.30	0.19	0.13
3	6	0.28	0.01	−0.12	0.28
4	7	0.11	0.13	0.05	0.12
5	3	0.00	0.41	0.29	0.12
6	5	0.45	0.24	0.09	0.33
7	1	—	—	—	—
8	6	0.64	−0.13	−0.27	0.19
12	6	0.30	−0.05	−0.17	0.24
20	1	—	—	—	—
24A	11	0.22	−0.13	−0.20	0.11
24B	5	−0.07	0.05	−0.10	0.22
F21	5	0.72	−0.58	**−0.76**	0.30
F23	5	0.09	−0.11	−0.25	0.22
F25	5	0.06	−0.11	−0.25	0.15
33	8	0.82	−0.52	**−0.64**	0.19
Sibling Group 1	6	0.52	−0.31	**−0.24**	0.08
Sibling Group 2	14	0.55	−0.20	**−0.21**	0.08

Population estimates

Relatedness	F_{IT}	F_{IS}	F_{ST}
0.25 ± 0.12	0.15 ± 0.05	−0.070 ± 0.073	0.209 ± 0.086
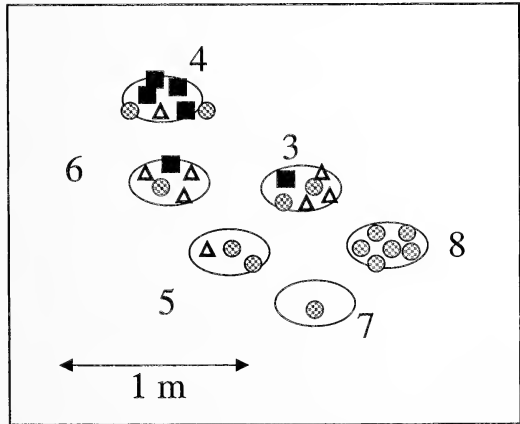
Figure 2.—Kinship assignment based on allele combinations of clusters 3–8. Ellipses indicate juvenile clusters on separate plants. Individuals belonging to sibling group 1 are depicted with squares (■), sibling group 2 members with circles (●), and non-assigned individuals by triangles (△). Two centers of distribution can be recognized.

dividuals that were not regrouped were omitted from the population analysis to avoid biasing population estimates. The two predicted sibling groups showed a relatedness estimate of $R \approx 0.50$ and a significant excess of heterozygotes, $F < 0$ (Table 2). However, the genotype composition of sibling group 2 revealed that it does not consist of only full-siblings. At least one second mating must be assumed. Each group has a center of origin, and juveniles of the two groups mix (Fig. 2).

Kinship analysis of cluster 12 showed two significant full-sibling groups for individuals 1, 3 and 5, and for 4 and 7, respectively. In the upper wadi, the kinship analysis for the group aggregation 24A, 24B, F21, F23 and F25 did not give unequivocal results. The distribution of rare alleles indicated, as previously, mixing of juveniles but an individual assignment to sibling groups was only possible for the F21 cluster, which indicated individuals of a single sibling group. The analysis gave ambiguous results for the remaining individuals due to the lack of rare-allele varia-

Table 2.—A comparison of within-locality genetic structure in sub-social and social spiders. Genetic variance components are divided into three categories and refer to the location at which an individual can be found relative to the population at large: (i) variance among kin-groups (after juvenile dispersal); (ii) demic effects at a locality (intra-locality Wahlund effect); and (iii) more than one genetically independent population unit within a locality (i.e., closed colonies).

| Species | Source of variance, among: | | | Reference |
	(i) Kin groups	(ii) Demes	(iii) Closed colonies	
Sub-social species				
Eresus cinnaberinus	Yes	No	No	Johannesen et al. 1998
Stegodyphus. lineatus	Yes	Yes	No	Johannesen & Lubin 1999
Social species				
Stegodyphus sarasinorum	?	Yes	Yes	Smith & Engel 1994
Anelosimus eximius	?	Yes	Yes	Smith 1986; Smith & Hagen 1996
Agelena consociata	?	Yes	Yes	Roeloffs & Riechert 1988; Riechert & Roeloffs 1993
Achaearanea wau	?	Yes	?	Lubin & Crozier 1985

tion. All individuals of cluster 33 indicated full-siblings. However, individual 4 is more likely a half-sibling to the remaining individuals, as indicated by the *Pep-B1* genotype. Combining the kinship analysis and F_{group} estimators suggests that most clusters consisted predominantly of siblings.

DISCUSSION

Intrademic structure of *S. lineatus*.—We found that despite juvenile nest relocation within the first months of leaving the maternal nest (Ward & Lubin 1993; Lubin et al. 1998), most juveniles remained distinctly clustered and did not disperse over greater distances. Several months after leaving the maternal nest, juveniles in isolated clusters consisted mostly of sibling groups, whereas larger aggregations of juveniles originated from several parental pairs. In these larger groups, juveniles of different parentage can mix. However, even within such aggregations, sibling groupings could be identified. Furthermore, we found evidence for the occurrence of multiple mating; thus, some of the variation is likely to be due to multiple fathers. The suggestion that multiple mating is not uncommon derives also from field studies showing a high frequency of male infanticide and probable re-mating in a natural population (Schneider 1997; Schneider & Lubin 1996, 1997).

In the present study, the lack of heterozygotes at the population level suggests that mating-dispersal did not take place throughout the population. If mating is random throughout a population, the population at large should obey Hardy-Weinberg proportions. Indeed, if a population is subdivided into family units, the population inbreeding coefficient is expected to be very slightly negative, i.e., showing an excess of heterozygotes (Cockerham 1969; Rasmussen 1979). A heterozygote deficit for an entire population that is divided into sibling groups is a strong indication for non-random mating within the population and, therefore, of population sub-structuring. Thus we conclude that *S. lineatus* juveniles settle, and later mate, largely in the vicinity of the maternal nest. The existence of clusters of siblings suggest that new groups arise by single females colonizing new nesting sites.

Despite male dispersal during the mating period (Schneider & Lubin 1996), female group founding must have a greater relative impact on population structure because the propagule-type of cluster founding (Slatkin 1977), combined with generally philopatric behavior, enhances genetic differences among groups more rapidly than male mating-dispersal can break them down. Furthermore, if females disperse to previously empty sites, then the two phenomena of female philopatry and female dispersal will combine to create neighborhood-structured demes. Therefore, occasional dispersal by females to new local-

ities away from the cluster does not conflict with the observed structure. Female distributions are the basis for kin-groups. This is supported by a previous study of population structure, which showed that sibling groups could be found even among adult spiders and also suggested that male mating-dispersal was limited (Johannesen & Lubin 1999). The previous results may have been biased because spiders were sampled from long-lived Acacia trees, which are relatively uncommon habitats for *S. lineatus* in the Negev region. The two studies combined show that a stable environment is not necessary to create sub-structuring of a *S. lineatus* population. In addition, the present study shows that intrademic structure does not depend on the life stage sampled: juvenile and adult populations exhibited similar population structures. Rather, population sub-structuring into sibling groups is likely to be an inherent consequence of philopatric breeding and dispersal behavior.

The type of population structure seen in *S. lineatus,* where spiders occur in family neighborhoods and further population subdivision results from restricted movement of males, may lead to the differential proliferation of both kin-groups and population subsets. One may think of a *S. lineatus* population as a dynamic population where new patches arise constantly and old o nes disappear. Female group-founding and limited mating-dispersal within the population lead to the differential distribution of genetic variation within populations This pattern can be seen in other populations in the Negev (Johannesen & Lubin 1999).

Intrademic structure and social spider evolution.—The genetic structure observed among *S. lineatus* clusters complies with predictions of increased intra-locality structure for social evolution. However, we need to know whether genetic similarity within groups per se can be extrapolated to provide a basis for the evolution of social behavior. If kin-groups in an open mating system are defined as population units then a significant among-group variance, i.e. similarity of group members, is inherent (e.g., Ingvarson & Giles 1999), but does not necessarily imply an advantage to sociality. Genetic indices can be used to infer the origin and mode of individual distribution patterns (and structuring processes) and may as such, be more informative explaining social spider evolution than merely similarity of group members.

Common for social spiders is the establishment of new colonies or populations by mated females or by several related individuals (Vollrath 1982; Lubin & Robinson 1982), and the presence of closed colony clusters. In other words, genetic similarity is achieved by female lineages (propagule migration model), not by migrants from different populations mating randomly in isolated populations (migrant-pool model). The former type of structuring process seems also true for the sub-social *S. lineatus,* albeit in an open system. A comparison of *S. lineatus* and another sub-social eresid, *Eresus cinnaberinus* (Olivier 1789) indicates that the genetic variance in *S. lineatus* is partitioned a step further than in *E. cinnaberinus,* where family groups are observed, but there is no intralocality subdivision (Johannesen et al. 1998). However, in neither *S. lineatus* nor *E. cinnaberinus* were localities divided into more than one population unit, as has been found in social spiders (Table 2). Intralocality differentiation also seems limited or lacking in two non-social species that have been investigated in more detail at the within population level. In *Pholcus phalangioides* (Fuesslin 1775) there is suggestive evidence that philopatry may cause some micro-structuring among cellar populations within the same building, but also that frequent dispersal breaks it down repeatedly (Schäfer et al. 2001). For *Atypus affinis* Eichwald 1830, no within-population divergence was observed. Structuring processes are active, however, at distances of a few kilometres. Ballooning *A. affinis* probably seldom drift beyond the bounds of the population (Pedersen & Loeschcke 2001). In contrast, virtually no structure was detected in the excellent ballooner *Argiope trifasciata* (Forskal 1775) (Ramirez & Haakonsen 1999).

The four social species that have been investigated genetically, *Stegodyphus sarasinorum* Karsch 1891, *Anelosimus eximius* (Keyserling 1884), *Agelena consociata* Denis 1965 and *Achaearanea wau* Levi et al. 1982 have taken population subdivision one step further than *S. lineatus* by creating a closed genetic system of regularly inbreeding colonies. The general lack of allozyme allelic variation in social relative to sub-social species may also be evidence for a process of group closure

(Table 2). We emphasize that Table 2 at present is only suggestive and that three caveats should be noted: 1) The family component in the sub-social species can be estimated because individuals could be assigned to specific grid-positions. This has not been possible in the social species where individuals were taken at large from a colony and within-colony family components have not been determined. 2) The term "closed colony" refers to at least two genetically independent colony clusters at one locality. Many localities probably contain clusters derived from a single founding event. Because of the general lack of genetic polymorphism in social spiders, it could not be determined if these colonies have diverged into independent population units or not. 3) Because the localities of social spiders may consist of more than one population unit, the deme genetic variance is given *a priori*.

A closed population structure will generate extreme variances between groups. If groups have different relative fitness, this may result in selection among groups. Groups with higher productivity (due to cooperation) should produce more young, and therefore more dispersing propagules, than groups lacking this trait. To avoid invasion of selfish individuals, high population turnover (Avilés 1993) and dispersal to establish new trait groups (Sober & Wilson 1998) are essential. Two of the three social species of *Stegodyphus* were shown to experience high population turnover (Seibt & Wickler 1988; Crouch & Lubin 2000). Further evidence for a change in population system, from an open system to a closed one, comes from the study of female-biased sex ratios in social spiders. High population turnover alone is not sufficient to produce these ratios. Two additional components, group-level selection and enough population subdivision to create a ratio of the genetic variances favorable to the group level, are required (Avilés 1993). Intercolony selection can only take place once closed colonies have been established (Avilés 1997).

The genetic data presently compiled on social and sub-social spiders allows preliminary comparisons of genetic patterns among species of different social levels relative to their breeding behavior (Table 2). One possible test to evaluate the significance of breeding structure in spider social evolution would be to compare the population genetic structure of social and sub-social species with communal non-social species. The latter form coherent groups, and perhaps even kin-groups, but are unlikely to inbreed. A comparison of genetic systems might identify patterns for the elucidation of underlying evolutionary processes. However, one should keep in mind that patterns do not create processes, rather patterns may be used only to infer processes (Templeton 1998).

The central unsolved questions are thus how and why do open systems become closed, what ecological conditions make individuals refrain from dispersal altogether and remain clustered (see discussions in Avilés & Gelsey (1998) and Avilés (1999), and is a closed system required for the evolution of sociality in spiders? Thus, in a genetic context, one needs to distinguish between traits leading to and resulting from demic structure.

ACKNOWLEDGMENTS

LITERATURE CITED

Avilés, L. 1993. Interdemic selection and sex ratio: a social spider perspective. American Naturalist 142:320–345.

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498, *In* Social Behavior in Insects and Arachnids. (J. Choe & B. Crespi, eds.). Cambridge University Press, Cambridge, Mass.

Avilés, L. 1999. Cooperation and non-linear dynamics: ecological perspective on the evolution of sociality. Evolutionary Ecology Research 1: 459–477.

Avilés, L. & G. Gelsey. 1998. Natal dispersal and demography of a subsocial *Anelosimus* species and its implications of sociality in spiders. Canadian Journal of Zoology 76:2137–2147.

Buskirk, R.E. 1981. Sociality in the Arachnida. Pp. 281–367, *In* Social Insects (H. R. Hermann, ed.) Academic Press, New York.

Chesser, R.K. 1991. Gene diversity and female philopatry. Genetics 127:437–447.

Crouch, T.E. & Y. Lubin. 2000. Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae). Journal of Arachnology 28:158–168

Cockerham, C.C. 1969. Variance of gene flow frequencies. Evolution 23:72–84.

Ingvarson, P.K. & B.E. Giles. 1999. Kin-structured colonization and small-scale genetic differentiation in *Silene dioicia*. Evolution 53:605–611.

Johannesen, J., T. Baumann, A. Seitz & M. Veith. 1998. The significance of relatedness and gene flow on population genetic structure in the subsocial spider *Eresus cinnaberinus* (Araneae: Eresidae). Biological Journal of the Linnean Society 63:81–98.

Johannesen, J. & Y. Lubin. 1999. Group founding and breeding structure in the subsocial spider *Stegodyphus lineatus* (Eresidae). Heredity 82:677–686.

Kullmann, E. & W. Zimmermann. 1975. Regurgitationsfütterungen als Bestandteil der Brutfürsorge bei Haubennetz- und Röhrenspinnen (Araneae, Theridiidae und Eresidae). Proceedings of the 6th International Arachnological Congress, Amsterdam.

Louis, E.J. & E.R. Dempster. 1987. An exact test for Hardy-Weinberg and multiple alleles. Biometrics 43:805–811.

Lubin, Y. D. & R. H. Crozier 1985. Electrophoretic evidence for population differentiation in a social spider *Achaearanea wau* (Theridiidae). Insectes Sociaux 32:297–304.

Lubin, Y.D., J. Hennicke & J. Schneider. 1998. Settling decisions of dispersing *Stegodyphus lineatus* (Eresidae) young. Israel Journal of Zoology 44:217–225.

Lubin, Y.D. & M.H. Robinson. 1982. Dispersal by swarming in a social spider. Science 216:319–321.

Pedersen, A.a. & V. Loeschcke. 2001. Conservation genetics of peripheral populations of the mygalomorph spider *Atypus affinis* (Atypidae) in northern Europe. Molecular Ecology 10:1133–1142.

Queller, D.C. & K.F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution 43:258–275.

Ramirez, M.G. & K.E. Haakonsen. 1999. Gene flow among habitat patches on a fragmented landscape in the spider *Argiope trifasciata* (Araneae: Araneidae). Heredity 83:580–585.

Rasmussen, D.I. 1979. Sibling clusters and genotypic frequencies. American Naturalist 113:948–951.

Raymond, M. & F. Rousset. 1995. GENEPOP (V.1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Riechert, S.E. & R.M. Roeloffs. 1993. Evidence for and consequences of inbreeding in the cooperative spiders. Pp. 283–303, *In* The Natural History of Inbreeding and Outbreeding: Theoretical and Emperical Perspectives. (N. W. Thornhill, ed.). Chicago University Press, Chicago.

Roeloffs, R.M. & S. E. Riechert. 1988. Dispersal and population genetic structure of the cooperative spider, *Agelena consociata,* in west African rainforest. Evolution 42:173–183.

Schäfer, M.A., A. Hille & G.B. Uhl. 2001. Geographic patterns of genetic subdivision in the cellar spider *Pholcus phalangioides* (Araneae). Heredity 86:94–102.

Schneider, J.M. 1995. Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). Insects Sociaux 42:237–248.

Schneider, J.M. 1997. Timing of maturation and the mating system of the spider, *Stegodyphus lineatus* (Eresidae): how important is body size. Biological Journal of the Linnean Society 60:517–525.

Schneider, J.M. & Y. Lubin. 1996. Infanticidal male eresid spiders. Nature 381:655–656.

Schneider, J.M. & Y. Lubin. 1997. Infanticide by males in a spider with suicidal maternal care, *Stegodyphus lineatus* (Eresidae). Animal Behavior 54:305–312.

Seibt, U. & W. Wickler. 1988. Bionomics and family structure of 'Family Spiders' of the genus *Stegodyphus,* with special reference to the African species *S. dumicola* and *S. mimosarum.* Verhandlungen Naturwissenschaftlichen Hamburg (NF) 30:255–303

Slatkin, M. 1977. Gene flow and genetic drift in a species subject to frequent local extinctions. Theoretical Population Biology 12:253–262

Smith, D.R.R. 1986. Population genetics of *Anelosimus eximius* (Araneae, Theridiidae). Journal of Arachnology 14:201–217.

Smith, D.R. & M.S. Engel. 1994. Population structure in an Indian cooperative spider, *Stegodyphus sarasinorum* Karsch (Araneae, Eresidae) Journal of Arachnology 22:108–113.

Smith, D.R. & R.H. Hagen. 1996. Population structure and interdemic selection in the cooperative spider *Anelosimus eximius.* Journal of Evolutionary Biology 9:589–608.

Sober, E., & D.S. Wilson. 1998. Unto Others. The Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge.

Swofford, D.L. & R.B. Selander. 1989. Biosys-1: a Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. Journal of Heredity 72:281–283.

Templeton, A.R. 1998. Species and speciation: geography, population structure, ecology, and gene trees. Pp. 32–43, *In* Endless Forms: Species and Speciation. (D. J. Howard & S. H. Berlocher, eds.). Oxford University Press, New York.

Vollrath, F. 1982. Colony formation in a social spider. Zeitschrift für Tierpsychologie 60:313–324.

Ward, D. & Y. Lubin. 1993. Habitat selection and the life history of a desert spider, *Stegodyphus*

lineatus (Eresidae). Journal of Animal Ecology 62:353–363.

Weir, B. S. 1991. Genetic Data Analysis. Sinauer, Sunderland.

Weir, B. S. & C. C. Cockerham. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370.

Appendix. Genotypes of seven polymorphic loci in *S. lineatus* juveniles smapled at Sede Boker. Missing genotypes were too weak to score. Allele designations are relative distances, except for *esterase* which was run in two buffers and alleles were given numbers according to their mobility.

Cluster1

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	44	100100	100100	100100		
2	100113	45	100100	90100	100100	94106	77100
7	100100	44	100100	90100	100100	100106	10010

Cluster 2

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	44	100100	90100	100100	94100	100100
3	100113	44	100100	100100	100100	9494	7777
5	93100	55	100100	100100	100100	100106	7777
6	100113	44	100100	90100	100100	100106	7777

Cluster 3

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	45	100100	100100	100100	100100	7777
2	100113	24	100100	90100	100100	100100	7777
3	100100	44	100100	100100	100100	100100	77100
4	100100	44	100100	100100	100100	100100	7777
5	100100	46	100100	100100	100100	100106	77100
6	100113	24	100100	9090	100100	100100	77100

Cluster 4

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	44	100100	100100	100100	100100	7777
2	100100	46	100100	100100	100100	100100	77100
3	100100	46	100100	100100	100100	106106	7777
4	100100	46	100100	90100	100100	100106	7777
5	100100	44	100100	100100	100100	106106	77100
6	100113	24	100100	90100	100100	100100	77100
7	100113	24	100100	9090	100100		7777

Cluster 5

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	113113	24	100100	90100	100100	100100	77100
3	100100	44	100100	100100	100100	100100	7777
4	100100	24	100100	9090	100100	100100	100100

Cluster 6

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	44	100100	100100	100100	100100	7777
2	100100	44	100100	100100	100100	100100	7777
3	100100	46	100100	100100	100100	100106	77100
4	100100	44	100100	9090	100100	100100	77100
5	100113	44	100100	100100	100100	100100	7777

Cluster 7

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100113	44	100100	100100	100100	100100	77100

Cluster 8

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100113	24	100100	9090	100100	100100	7777
2	113113	24	100100	90100	100100	100100	100100
3	100113	44	100100	9090	100100	100100	100100
4	100113	44	100100	9090	100100	100100	100100
5	100113	44	100100	90100	100100	100100	77100
6	100113	44	100100	9090	100100	100100	77100

Cluster 12

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100113	45	100100	100100	100100	106106	7777
3	100113	45	100100	100100	100100	106106	7777
4	100113	44	100100	90100	100100	106106	77100
5	100100	44	100100	100100	100100	106106	7777
6	100100	44	100100	100100	100100	100106	77100

Cluster 20

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	45	100100	100100	100100	106106	77100

Cluster 24A

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	45	100100	100100	100100	100106	7777
2	100113	55	100100	100100	100100	100100	77100
3	100113	45	100124	100100	100100	94106	77100
4	100100	55	100100	100100	87100	100100	77100
5	100113	45	100124	100100	100100	100100	7777
6	100100	55	100100	90100	100100	100100	7777
7	100113	45	100124	90100	100100	100100	77100
8	100100	45	100124	100100	100100	94100	77100
9	100100	55	100124	100100	100100	100100	7777
10	100100	44	100100	100100	100100	100106	77100
11	100100	55	100100	100100	100100	100106	7777

Cluster 24B

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	44	100100	90100	87100	100100	77100
2	113113	55	100100	100100	100100	100100	10010
3	100100	44	100100	100100	87100	100106	77100
4	100100	44	100100	100100	100100	100106	77100
5	100113	44	100100	90100	100100	100106	77100

Cluster F21

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100113	45	100100	90100	100100	100106	7777
2	100100	44	100100	90100	100100	100106	7777
3	100100	45	100100	90100	100100	100106	7777
4	100100	44	100100	90100	100100	100106	7777
5	100100	45	100100	90100	100100	100106	7777

Cluster F23

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100113	45	100124	100100	100100	100100	77100
2	100113	44	100100	100100	100100	100106	7777
3	100100	55	100100	100100	100100	100100	77100
4	100100	45	100100	90100	100100	100106	77100
5	100100	55	100100	90100	100100	100100	77100

Cluster F25

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	55	100100	100100	87100	100106	77100
2	100113	44	100100	100100	100100	94106	77100
3	100100	55	100100	100100	100100	100106	77100
4	100113	44	100100	100100	100100	100106	7777
5	100100	45	100100	100100	87100		

Cluster 33

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
1	100100	45	100124	100100	100100	9494	77100
2	100100	55	100100	100100	100100	9494	77100
3	100100	45	100124	100100	100100	9494	77100
4	100100	45	100124	100100	100100	94106	77100
5	100100	45	100124	100100	100100	9494	77100
6	100100	55	100100	100100	100100	9494	77100
7	100100	55	100124	100100	100100	9494	77100
8	100100	55	100124	100100	100100	9494	77100

SHORT COMMUNICATION

ON THE GENUS *EILICA* (ARANEAE, GNAPHOSIDAE) FROM ARGENTINA

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ABSTRACT. *Eilica pomposa* new species, from Buenos Aires, Argentina, and the male of *E. uniformis* (Schiapelli & Gerschman 1942) are described for the first time. New records from Argentina for *E. uniformis*, *E. modesta* and *E. trilineata* are included.

Keywords: *Eilica*, Gnaphosidae, new species, Neotropical region

The genus *Eilica* Keyserling 1891 can be easily distinguished from other gnaphosids by the presence of two or three translucent laminae on the cheliceral retromargin (Platnick 1975), similar to the lamina found in the closely related genus *Callilepis* Westring. These laminae are probably associated with their preference for preying on ants (Goloboff 2000). The genus is represented in Argentina by four species: *E. modesta* Keyserling 1891, *E. trilineata* (Mello-Leitão 1941), *E. uniformis* (Schiapelli & Gerschman 1942) (Platnick 1975, 1985; Platnick & Shadab 1981; Goloboff 2000) and *E. myrmecophila* (Simon 1903) (Platnick 1985; Platnick & Shadab 1981). Recent collecting with pitfall traps in Córdoba and Buenos Aires provinces has resulted in large samples of previously poorly-known spiders, among which are a new species of *Eilica* and the previously unknown male of *E. uniformis*, which are described below. The distribution of the species of *Eilica* in Argentina is shown in Fig. 1.

METHODS

All specimens examined are deposited in Museo Argentino de Ciencias Naturales (MACN, Cristina Scioscia), Facultad de Ciencias Exactas de Córdoba (FCEC, Luis Acosta) and Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA, Sergio Roig-Juñent). The format of descriptions follows Platnick (1975) and Brescovit & Höfer (1993). Measurements are in millimeters.

Eilica uniformis (Schiapelli & Gerschman)
Figs. 1–4

Laronia uniformis Schiapelli & Gerschman 1942: 330, figs. 17, 19 (female holotype from Colonia Dora, Santiago del Estero, Argentina, in MACN, examined); Gerschman & Schiapelli 1967: 201, figs. 17–20.
Eilica uniformis: Platnick 1975: 9, figs. 18–19.

Diagnosis.—Males are very similar to those of *E. rufithorax* (Simon 1892) but can be distinguished by their smaller median apophysis and by the pattern of light and dark areas on the dorsum of the abdomen.

Description.—*Male:* (Chancaní). Total length 3.08. Carapace 1.24 long, 0.94 wide. Length femur/tibia: I 0.82/0.62; II 0.70/0.52; III 0.60/0.42; IV 0.90/0.72. Carapace light brown medially, darker, striped laterally. Abdomen with dorsal distinctive pattern of light areas (Fig. 2). Palp (Figs. 3, 4): Tibial apophysis long, bent. Copulatory bulb: embolus with apical projecting lamella on base. Median apophysis short, bent. Leg spination not provided because in both specimens most spines are lost and their insertions are not distinctly visible.

Female: Described by Schiapelli & Gerschman (1942), Gerschman & Schiapelli (1967), and Platnick (1975).

Other material examined.—ARGENTINA: *Chubut:* Puerto Lobos, Jan. 1975, (E.A. Maury, MACN), 1♀. *Córdoba:* Chancaní, 19 Nov.–23 Dec. 1993, 1♂1♀ (C. Mattoni, MACN), 1♂2♀ (C. Mat-

toni, FCEC). *Misiones:* Santa María, 1944 (J.M. Viana, MACN), 1♀; Puerto Iguazú, 1954 (Schiapelli & Gerschman, MACN), 1♀; Puerto Libertad, 1953 (Schiapelli & Gerschman, MACN), 1♀.

Distribution.—Known only from Argentina (Fig. 1).

Eilica pomposa new species
Figs. 5–7

Type.—Male holotype from a community of *Baccharis salicifolia* (chilca) in Reserva Natural Otamendi, Buenos Aires province, Argentina, 18 March 1998 (Belén Fuentes and Osvaldo Di Iorio, MACN 2780).

Etymology.—The specific name is from the Latin word *pompa*, which means ostentation.

Diagnosis.—*Eilica pomposa* is closest to *E. modesta*, but it can be distinguished by having a larger median apophysis and a longer and pointed tibial apophysis.

Description.—*Male* (holotype): Total length 3.10. Carapace 1.43 long, 1.08 wide. Length femur/tibia: I 0.90/0.73; II 0.70/0.53; III 0.73/0.52; IV 1.00/0.88. Palp description: protruding portion of embolar base twisted, median apophysis large, thick, curved. Tibial apophysis elongate, curved, pointed (Figs. 6, 7). Leg spination: Femora: I d 0-1-1-0; II d 0-1-1-0; III d 0-1-1-0, p 1 ap; IV d 0-1-1-0, r 1 ap. Tibiae: I v 0-0-r1-2; II v 0-r1-r1-2; III p 1-1-0-0, v 0-p1-2-2, r 0-0-d1-d1; IV r 0-0-d1-d1. Metatarsi: I v 0-2-r1-2 or v 0-p1-p1-2; II v 0-2-0-2 or v 0-2-r1-2; III p 1 ap., v 0-0-r1-2, r 1 ap.; IV p 1 ap., v 0-p1-p1-2, r 1 ap. Tarsi: IV v 0-0-2-2. Abdomen: Dorsal pattern of four pairs of white specks and several posterior dark lines (Fig. 5).

Female.—Unknown.

Other material examined.—A male from Argentina, Mendoza, Reserva Ñacuñán, 22 Nov. 1997 (S. Lagos, IADIZA), seems to belong to the same species although it is from a very distant locality (*ca.* 1000 km apart, see Fig. 1). Further collections may help to elucidate the actual distribution of the species.

ADDITIONAL RECORDS IN ARGENTINA

Eilica modesta—*Jujuy:* No specific locality, 17 Jan. 1966 (E.A. Maury, MACN), 1♀. *Córdoba:* Tanti, 1950 (J.M. Viana, MACN), 1♂; Calamuchita, 1955 (J.M. Viana, MACN), 2♀. *Buenos Aires:* Sierra de la Ventana, Dec. 1968 (E.A. Maury, MACN), 1♀; San Vicente, 1964 (Canto, MACN), 2♀. *Santiago del Estero:* No specific locality, March 1963 (Hepper, MACN), 1♀.

Eilica trilineata.—*Catamarca:* Capillitas, 1 Feb. 1981 (A. Roig, MACN), 2♂2♀. *San Juan:* Las Tumanas, 14 April 1979 (A. Roig, MACN), 1♀. *La Rioja:* Aimogasta, 1944 (J. Cáceres Freyre, MACN), 1♀.
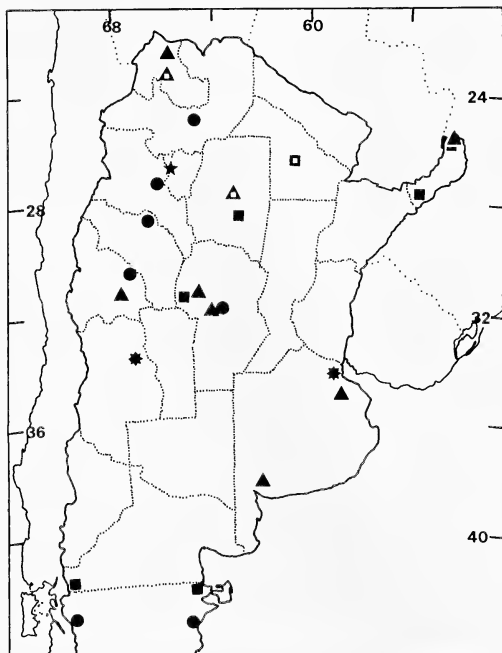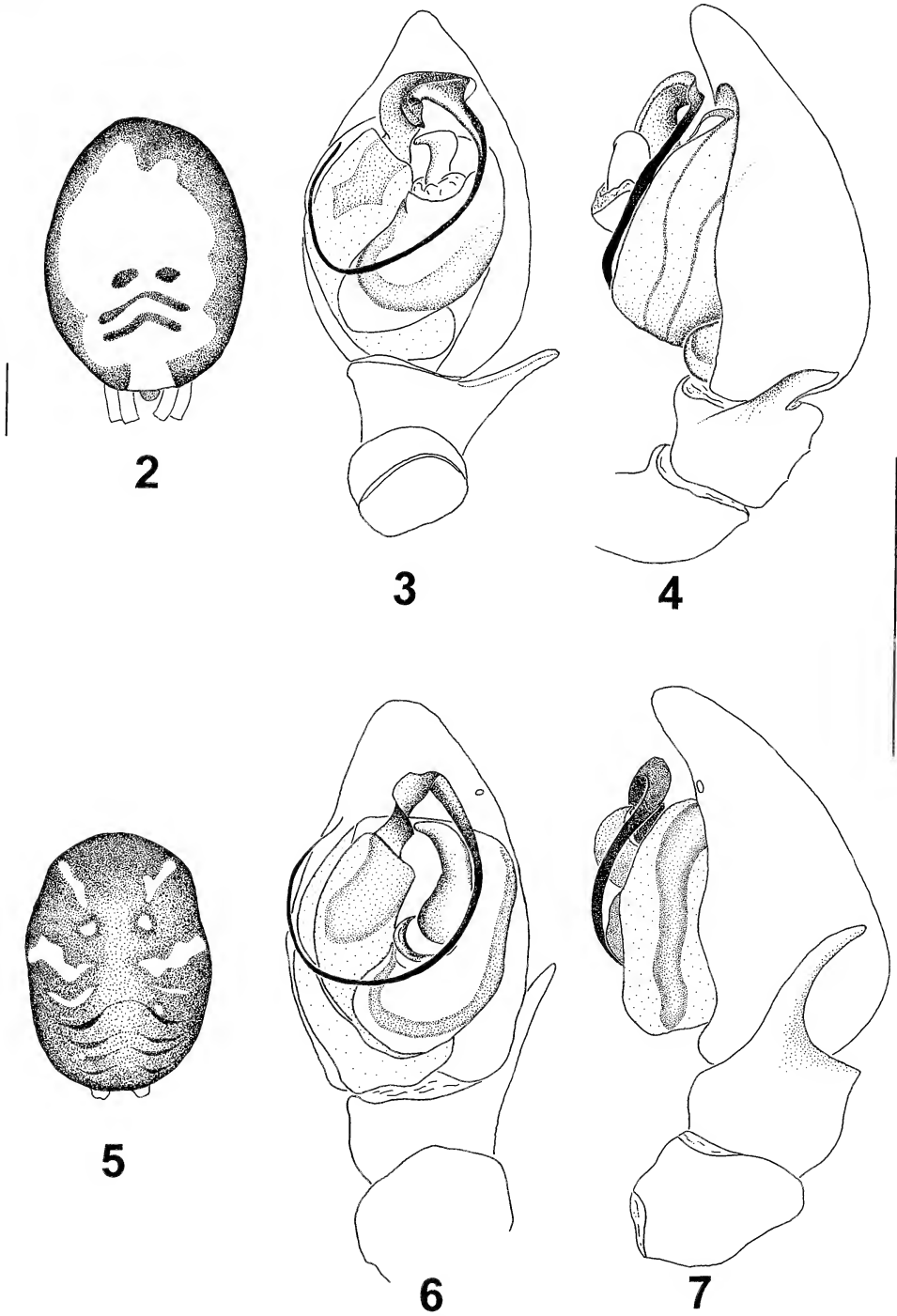
ACKNOWLEDGMENTS

Figure 1.—Distribution of the species of *Eilica* in Argentina. ▲ = *E. modesta*, ■ = *E. uniformis*, ● = *E. trilineata*, ∗ = *E. pomposa* new species, ★ = *E. myrmecophila*. Symbols with a white square inside indicate that the specific locality is not known. (Data from this paper and Platnick 1975, 1981, 1985.)

Figures 2–7.—2. *Eilica uniformis*, abdomen, dorsal view; 3. *E. uniformis*, palp, ventral view; 4. *E. uniformis*, palp, retrolateral view. 5. **Eilica pomposa** new species, abdomen, dorsal view; 6. **E. pomposa** new species palp, ventral view; 7. **E. pomposa** new species, palp, retrolateral view. Scale = 0.5 mm.

LITERATURE CITED

Brescovit, A.D. & H. Höfer. 1993. Aranhas dos gêneros *Lygromma* e *Eilica*, da Amazônia Central, Brasil (Araneae, Gnaphosidae). Iheringia, Série Zoologia 74:103–107.

Gerschman, B.S. & R.D. Schiapelli. 1967. El género *Laronia* Simon, 1892 (Araneae, Drassodidae). Acta Zoologica Lilloana 23:189–200.

Goloboff, P.A. 2000. The family Gallieniellidae (Araneae, Gnaphosoidea) in the Americas. Journal of Arachnology 28:1–6.

Platnick, N.I. 1975. A revision of the spider genus *Eilica* (Araneae, Gnaphosidae). American Museum Novitates 2579:1–19.

Platnick, N.I. 1985. Notes on the spider genus *Eilica* (Araneae, Gnaphosidae). Journal of the New York Entomological Society 93(3):1073–1081.

Platnick, N.I. & M.U. Shadab. 1981. On the spider genus *Eilica* (Araneae, Gnaphosidae). Bulletin of the American Museum of Natural History 170:183–188.

Schiapelli, R.D. & B.S. Gerschman. 1942. Arañas argentinas (1ª parte). Anales. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," 40:317–332.

SHORT COMMUNICATION

DISTINGUISHING THE FEMALES OF *TROCHOSA TERRICOLA* AND *TROCHOSA RURICOLA* (ARANEAE, LYCOSIDAE) FROM POPULATIONS IN ILLINOIS, USA

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The Palearctic lycosid species, *Trochosa ruricola* (De Geer 1778), is here recorded for the first time in the State of Illinois. It was previously known only from Massachusetts in the USA. The species is widely distributed in northern and middle Europe and Asia and was apparently introduced into Bermuda sometime prior to 1888 (Marks 1889; Banks 1902; Sierwald 1988). *Trochosa terricola* Thorell 1856 is considered a Holarctic species, occurring in northern Europe as well as in North America, from Alaska to Newfoundland and south to northern California, Arizona, south-central Texas, and Alabama (Brady 1979; Roberts 1985; Dondale & Redner 1990). Both *Trochosa* C.L. Koch 1847 species are common throughout much of their respective ranges in northern Europe and the British Isles (Roberts 1995). They are the most prevalent of the four European congeners in the British Isles where they often occur in sympatry (Roberts 1985; Edwards 1993).

Sometime prior to 1993, a thriving population of *T. ruricola* was discovered in Cape Cod, Massachusetts, which outnumbered the native *T. terricola* in pitfall trap samples by a ratio somewhat greater than 2:1 (Edwards 1993). In 1994, the first known specimens were collected in Canada (L'Acadie, Quebec) (Lalongé et al. 1997). During a 1999 biodiversity study (funded by Chicago Wilderness) within three forest preserves in Lake County, Illinois, both *T. ruricola* and *T. terricola* were discovered in sympatry. In this study, however, *T. terricola* outnumbered the non-native *T. ruricola* by a factor of approximately 2.5:1 (males–1.9:1; females–4.25:1). Edwards

(1993) distinguished *T. terricola* from *T. ruricola* by the absence or presence (both sexes and all instars in either case), respectively, of a claw on the palpal tarsus. *Trochosa ruricola* males were also distinguished by a unique ridge or carina at the base of the fang on the outer (convex) face and by a slight, anteriorly directed bend or curl of the apical portion of the embolus (Edwards 1993). In *T. terricola*, the ridge on the fang is lacking and the apical portion of the embolus forms a circular loop (Brady 1979; Edwards 1993). The Canadian researchers found only *T. ruricola* in Quebec samples (Lalongé et al. 1997).

In Lake County, Illinois pitfall trap samples from Grainger Woods, Elm Road, and Spring Bluff Forest Preserves, all *Trochosa* females and juvenile instars examined were equipped with a pectinate claw on the palpal tarsus. Grounded on Edwards' presence or absence characters, I began to assign all *Trochosa* females to *T. ruricola*, based on the presence of a palpal claw. However, in light of the dominance of *T. terricola* males in samples, I found it hard to believe that only *T. ruricola* females were subject to pitfall collection. After thorough reexamination of all *Trochosa* females, I discovered that, in some specimens, there was relatively wide and usually unbroken, light-colored submarginal band on the carapace (Fig. 1). In others, the band was somewhat narrower and broken in several places (Fig. 2) or was barely discernible. Reexamination of the males revealed a similar difference in banding patterns. In *T. ruricola* males, this band was relatively wide and often unbroken (Fig. 3) or, if broken, only faintly
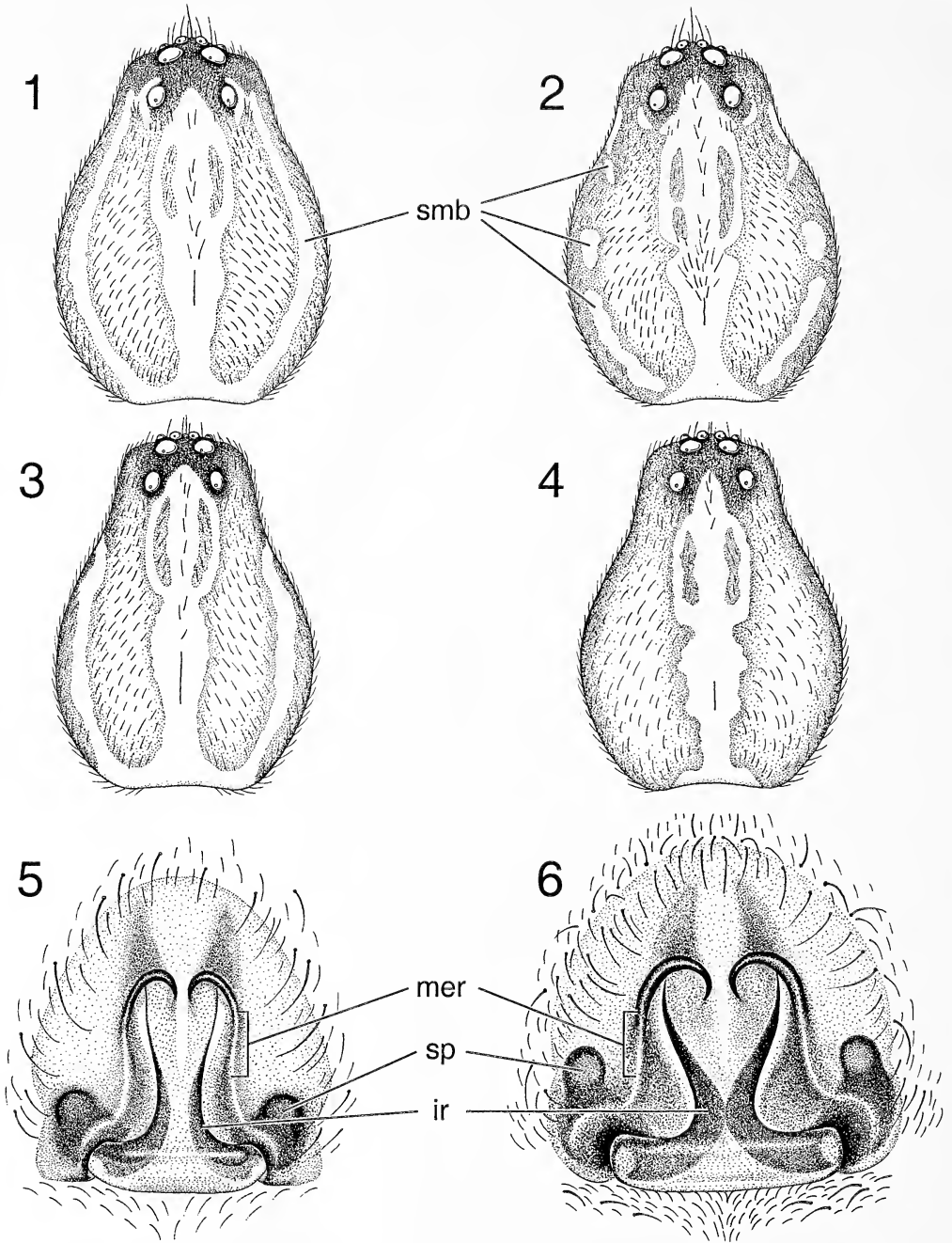
Figures 1–6.—*Trochosa ruricola* and *T. terricola* from Lake County, Illinois. 1, 3, 5, *T. ruricola*. 1. Female carapace; 3. Male carapace; 5. Epigynum, ventral. 2, 4, 6, *T. terricola*. 2. Female carapace; 4. Male carapace; 6. Epigynum, ventral. *Abbreviations:* ir = internal longitudinal ridge; mer = medial portion

so and in few places. In *T. terricola* males, the band was usually narrow and widely broken in several places by the dark pubescence of the submedial regions of the carapace or was not discernable (Fig. 4). Females were

tentatively separated on the basis of the similarity of their bands to the respective male pattern. Those with a wide and largely unbroken band were determined as *T. ruricola* and those without an apparent band or with a nar-

row, largely broken band determined as *T. terricola* (the submarginal bands of the *T. ruricola* specimens illustrated in Figs. 1 & 3 were unusually narrow).

Substantiation of the female submarginal band configurations appeared to be confirmed, not only by the corresponding male patterns, but also by the details of the ventral views of the respective epigyna (internal structural differences were found to be unreliable). Both Roberts' illustrations and those presented here clearly show that, in *T. ruricola*, the orientation of the spermathecae is directed lateroanteriad (obliquely oriented) to the termini of the transverse portion of the median septum (Fig. 5; compare to Roberts 1985, fig. 62c). In *T. terricola*, the orientation is directed anteriad to the termini (Fig. 6; compare to Roberts 1985, fig. 62e). In *T. ruricola*, the internal longitudinal ridges (darkened tube-like structures visible at the lateral edges of the longitudinal portion) are generally separated medially toward the posterior end of the longitudinal portion of the septum. They usually do not impinge on the posterior border of the transverse portion where they merge with the copulatory tubes (Fig. 5). In *T. terricola*, the internal ridges are usually contiguous (or nearly so) medially and are usually visible (ventral view) near the posterior border of the septum (Fig. 6). The transverse portion of the septum is relatively short (relative to the length of the longitudinal portion) and the anterior margins only slightly concave to moderately straight in *T. ruricola* (Fig. 5). By comparison, the transverse portion is relatively long and the anterior margins generally concave in *T. terricola* (Fig. 6). The median ectal rim portions of the paired hood cavities are directed posteriad (median lateral edges parallel) or medioposteriad in *T. ruricola* (Fig. 5; Roberts 1985, fig. 62c) but are usually directed lateroposteriad (oblique) in *T. terricola* (Fig. 6; Roberts 1985, fig. 62e).

Differentiation of the Lake County *Trochosa* females was generally conclusive by employing only the submarginal band character (epigynal characters were also used to confirm placement). However, this banding pattern may appear to be somewhat subjective to future workers if only females of one of the two species occur in northern Illinois samples. But even in *T. terricola* females with well-developed submarginal bands, the pattern is almost always widely broken in at least one region or more narrowly broken in several regions. In doubtful cases, especially in instances in which the epigyna of the respective females are very similar, a combination of the epigynal details (ventral view) and submarginal configuration may have to be used to separate the species. In regions of North America where *T. terricola* females lack a palpal claw, Edwards' characters should suffice to separate the two *Trochosa* females.

I would like to thank F. Catchpole for enlisting my services for the identification of Araneae from Lake County, C. Dondale for examining several *Trochosa* specimens and acknowledging the value of the submarginal band character, and M. Planoutene for producing the original artwork used in the illustrations. All Lake County *Trochosa* specimens, except those retained by the author, are deposited in the Field Museum, Chicago, Illinois.

LITERATURE CITED

Banks, N. 1902. Some spiders and mites from the Bermuda Islands. Transactions of the Connecticut Academy of Arts and Sciences 11:267–275.

Brady, A.R. 1979. Nearctic species of the wolf spider genus *Trochosa* (Araneae: Lycosidae). Psyche 86:167–212.

De Geer, C. 1778. Mémoires pour servir à l'histoire des insectes (Stockholm) 7(3–4):176–324.

Dondale, C.D. & J.H. Redner. 1990. The insects and arachnids of Canada, Part 17. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska, Araneae: Lycosidae, Pisauridae, and Oxyopidae. Research Branch, Agriculture Canada, Publication #1856:1–383.

Edwards, R.L. 1993. New records of spiders (Araneae) from Cape Cod, Massachusetts, including two possible European immigrants. Entomological News 104:79–82.

Koch, C.L. 1847. Die Arachniden, Nürnberg, Vierzehnter Band, pp. 89–210, Funfzehnter Band, pp. 1–136, Sechszehnter Band, pp. 1–80.

Lalongé, S., J.H. Redner, & D. Coderre. 1997. First Canadian records of *Trochosa ruricola* (De Geer), *Ostearius melanopygius* (O. Pickard-Cambridge), and *Dictyna decaprini* Kaston (Araneae: Lycosidae, Linyphiidae, Dictynidae, respectively). Canadian Entomologist 129:371–372.

Marks, G. 1889. A contribution to the knowledge of the spider fauna of the Bermuda Islands. Proceedings of the Academy of Natural Sciences, Philadelphia 1889:98–101.

Roberts, M.J. 1985. The Spiders of Great Britain and Ireland, Volume 1: Atypidae to Theridiosomatidae. Harley Books, Colchester, England.

Roberts, M.J. 1995. Collins Field Guide: Spiders of Great Britain & Northern Europe. Harper Collins Publishers, London.

Sierwald, P. 1988. Spiders of Bermuda. Nemouria: Occasional Papers of the Delaware Museum of Natural History 31:1–24.

Thorell, T. 1856. Recensio critica aranearum suecicarum quas descripserunt Clerckius, Linnaeus, de Geerus. Nova acta Regiae Societatis Scientarum Upsaliensis (3) 2(1):61–176.

SHORT COMMUNICATION

THE UNUSUAL EGG-ROD OF THE SPIDER
HOMALOMETA CHIRIQUI (ARANEAE, TETRAGNATHIDAE)
AND OTHER BIOLOGICAL DATA

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ABSTRACT. Field observations of *Homalometa chiriqui* (Araneae, Tetragnathidae), a common habitant in coffee plantations in Chiapas, México, provide biological information on this poorly known species. Collection data revealed several generations per year. The web architecture and microhabitat selection of young juveniles differ from those of older juveniles and adult females. Females deposit their eggs inside the retreat forming a straight cylindrical egg-rod.

Keywords: *Homalometa*, egg laying, web architecture, microhabitat, life cycle

The American orb weaver genus *Homalometa* Simon 1897 (Tetragnathidae) is known only from three species: *H. nigritarsis* Simon 1897 from the Lesser Antilles (Island of Saint Vincent and Martinique), Panama and México (Levi 1986); *H. chiriqui* Levi 1986 from Panama, Costa Rica and México (Ibarra & García 1998); and *H. nossa* Levi 1986 from Brazil.

Very little is known about the biology of this genus: females of *H. chiriqui* have been "collected to the side of orb—both specimens with a set of eggs under a leaf; in the orb at night" (Levi 1986). No more biological information on this genus occurs in the literature.

During studies on the diversity and ecology of spiders of coffee plantations in the Soconusco region of Chiapas, México (15°10'N, 92°20'W), we found *H. chiriqui* as a common resident in two coffee plantations. The spiders were collected by hand, after measuring the diameter of its web, the distance from it to the ground, and noting the placement and orientation of its web and retreat, and presence of eggs or spiderlings. Voucher specimens of these spiders were deposited in the Colección de Arañas del Sureste de México (ECO-TA-AR) of El Colegio de la Frontera Sur, Tapachula, Chiapas, México.

In a two-year monthly sampling we found 481 specimens: 414 juveniles on webs, and 67

adults (54 females, 13 males). These specimens were found between 800–1000 m above sea level. All age classes and both adult sexes were found almost all year round, as well as females with eggs or young spiderlings inside the retreats (Table 1). This shows clearly that this species has several generations per year.

There were differences in form and orientation of the web, as well as in the microhabitat selection for the placement of the web and its associated retreat among younger and older juveniles and adult females. Young juveniles spin their small (2–4 cm in diameter) symmetrical and almost horizontal orb webs on the upper side of a coffee leaf, supported mainly from its lateral borders, with the spider's retreat below the web, on the leaf upper surface, where the spiderling is found most of the time. Larger juveniles and adult females spin a vertical asymmetrical orb web on the side of a coffee leaf (Fig. 1), also supported by other leaves and branches, with a mean vertical diameter of 11 cm (5–20 cm). In this case the retreat is built on the underside of a leaf in front of the web's hub and slightly inclined to the vertical. A signal line leads from the hub of the web to the entrance of the retreat. The retreat is an elongated vertical vault made of a thin layer of silk, almost transparent, with one exit hole for the spider on the upper side and the entrance on the lower side
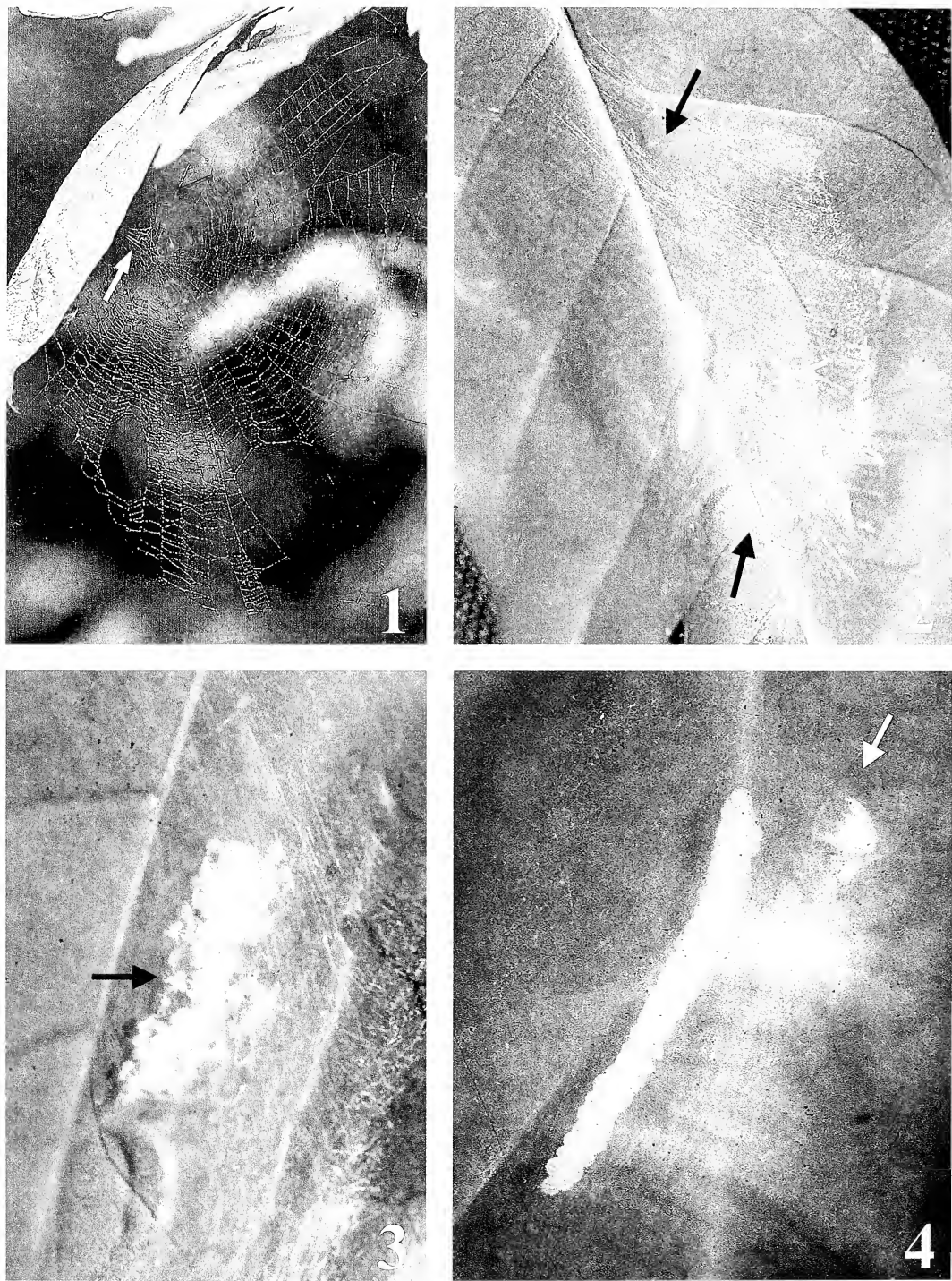
Figures 1–4.—*Homalometa chiriqui*, female web, retreat with female, egg-rod and spiderlings. 1. Vertical asymmetrical web among coffee leaves showing signal line (arrow); 2. Retreat on underside of coffee leaf showing egg-rod with female on side (white arrow), entrance (lower black arrow) and exit holes (upper black arrow); 3. Recently emerged spiderlings (arrow) around egg chorions and exuviae; 4. View of egg-rod in detail and female (arrow).

Table 1.—Accumulated monthly abundance of juveniles on webs and adults (by sex) of *H. chiriqui,* in a two-year sampling at two coffee plantations in the Soconusco region of Chiapas, Mexico. The number of females found with egg-rod or spiderlings is noted in parentheses.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Juveniles	59	20	71	16	26	8	11	22	97	10	43	31	414
Females	5 + (2)	1	4	(2)	1	2 + (4)	6 + (4)	(1)	1 + (2)	0	9 + (2)	8	37 + (17)
Males	0	1	0	1	3	1	1	0	2	0	4	0	13
Total	66	22	75	19	30	15	22	23	102	10	58	39	481

(Fig. 2). The spider (juvenile or adult) is normally inside the retreat, but it drops very quickly when slightly disturbed if without offspring. If with eggs or spiderlings, the female is more reluctant to abandon its retreat. The mean distance of the web to the ground was 135 cm for both small juveniles (35–204 cm) and larger juveniles and female adults (30–350 cm).

Adult females deposit their eggs inside the retreat, but they do not make a conventional egg-sac. Instead, they place the eggs in a line over a thin layer of silk, forming a straight cylindrical "rod," three to four eggs in width (Figs. 2, 4). The eggs adhere to one another and are supported by the basal thin layer of silk. This is an unusual way to arrange the eggs, and no other species has been reported in the literature to put its eggs in a rod exactly like *H. chiriqui*. Females of the uloborid genus *Miagrammopes* and some species in the genus *Argyrodes* make cylindrical egg-sacs, but in these cases the eggs are visibly wrapped with silk (Exline & Levi 1962; Opell 1984, 1989). In contrast, the egg-rod of *H. chiriqui* did not appear to be covered by silk. After hatching, the young spiderlings of *H. chiriqui* stay in the rod by the side of the egg chorions and first exuviae, with the female guarding them (Fig. 3) until they molt and become larger. Then, they began to move on the retreat until they abandon it.

The change in the web architecture from horizontal and symmetrical webs (in young juveniles) to vertical and asymmetrical webs (in older juveniles and adult females) suggests that—in this taxonomic context—vertical and asymmetrical are the apomorphic conditions. It is possible that the vertical asymmetrical web and the egg-rod constitute generic synapomorphies that could be tested when more information on the other species of this genus be available.

LITERATURE CITED

Exline, H. & H.W. Levi. 1962. American spiders of the genus *Argyrodes* (Araneae, Theridiidae). Bulletin of the Museum of Comparative Zoology 127:75–204.

Ibarra-Núñez, G. & J.A. García-Ballinas. 1998. Diversidad de tres familias de arañas tejedoras (Araneae: Araneidae, Tetragnathidae, Theridiidae) en cafetales del Soconusco, Chiapas, México. Folia Entomológica Mexicana 102:11–20.

Levi, H.W. 1986. The Neotropical orb-weaver genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae). Bulletin of the Museum of Comparative Zoology 151:91–215.

Opell, B.D. 1984. Eggsac differences in the spider family Uloboridae (Arachnida: Araneae). Transactions of the American Microscopical Society 103:122–129.

Opell, B.D. 1989. Do female *Miagrammopes animotus* (Araneae, Uloboridae) spin color-coordinated egg sacs? Journal of Arachology 17:108–111.

Simon, E. 1897. On the spiders of the Island of St. Vincent. Proceedings of the Zoological Society of London 1897:860–890.

BOOK REVIEWS:

NEW VOLUMES ON THE "MINOR" ARACHNID ORDERS

The Biology of Camel-Spiders (Arachnida, Solifugae). **Fred Punzo**. 1998. Kluwer Academic Publishers, Norwell, Massachusetts. 301 pp. ISBN 0-7923-8155-6. US$135.00 (hard cover).

Whip Spiders (Chelicerata: Amblypygi). Their Biology, Morphology and Systematics. **Peter Weygoldt**. 2000. Apollo Books, Stenstrup, Denmark. 163 pp. ISBN 87-88757-6-3 US$43.00 (DKK 320.00) (hard cover).

Hormiga (2000) recently attributed the dwindling number of publications on the "minor" arachnid orders (in decreasing number of described species—Opiliones, Pseudoscorpiones, Scorpiones, Solifugae, Schizomida, Amblypygi, Uropygi, Palpigradi, Ricinulei)—to two factors. First, these orders are less diverse, collectively comprising only 12.5% of arachnid species, compared with the megadiverse Acari and Araneae, containing some 87.5% (M.S. Harvey unpubl. data). Second, there has been an alarming decline in specialists on these taxa, despite the fragmentary knowledge about most aspects of their biology. At a time when major synthetic publications on the biology of the minor orders are as scarce as the specialists working on them, it is gratifying to report on new volumes that will hopefully restore interest and perhaps stimulate the development of new expertise in some of these intriguing groups.

As noted by Hormiga (2000), Tome VI of Grassé's (1949) *Traité de Zoologie* remains the standard text for the anatomy and biology of most of the minor orders, only two of which have been dealt with in more recent volumes: Pseudoscorpiones (Weygoldt 1969); Scorpiones (Polis 1990). Until recently, pseudoscorpions remained the most "accessible" of the minor orders, for which both a comprehensive synthesis of the biology (Weygoldt 1969) and an up-to-date, fully referenced taxonomic catalogue (Harvey 1990) were available.

Probably due to their medical importance, scorpions have enjoyed disproportionate attention, given that they represent only the third most speciose of the minor orders. A resurgence in studies on scorpions has occurred in the decade since publication of the volume by Polis (1990), culminating in the recent publication of another two volumes, presenting current research in scorpion biology (Brownell & Polis 2000) and cataloguing the taxonomic diversity of the order (Fet et al. 2000). A third volume, dealing with all aspects of scorpion biology, from taxonomy, through ecology to neurophysiology, has just been published (Fet & Selden 2001).

It was hoped that the publication of three volumes on Chelicerata in the series on *Microscopic Anatomy of Invertebrates* (Harrison & Foelix 1999) would provide an update of the information provided in Grassé's (1949) Tome VI for the remaining minor orders. Unfortunately, these volumes dealt only with the Acari, Araneae and Scorpiones, while omitting eight of the minor orders altogether (Hormiga 2000). However, two new volumes, which are the subject of this review, should redress this void for the Solifugae and Amblypygi, two of the smaller and more enigmatic orders for which no synthetic treatments were previously available.

The first of these volumes, *The Biology of Camel-Spiders*, has already received a thorough review by Hormiga (2000); what follows shall serve merely to supplement the latter. In

accordance with the previous reviewer, I am commending the author for filling a notorious gap in the arachnological literature by summarizing available knowledge on Solifugae into a single, clearly written volume. Regrettably, poor production by the publishers, coupled with various inconstencies, errors and omissions in the content, detract from otherwise fascinating subject matter.

Hormiga (2000) has already lamented the poor production of this volume, which is peppered with typographical errors, misaligned text, oddly positioned blank spaces, scientific binomens not set in different font style, etc. Treatment of the illustrations is particularly appalling. Some are unnecessarily large (p. 43) while others are poorly reproduced from adequate originals (p. 37). Still others are awful regardless of size or reproduction (p. 181). Several are not centered on the page (p. 22) or leave large blank spaces between the illustration and the text (pp. 15, 220). In many cases, the text of the illustrations is too large (p. 52).

Further criticisms concern aspects of the content. Eight chapters deal in somewhat haphazard fashion with the following topics: introduction to Solifugae, including mythology and folklore (10 pp.); functional anatomy and physiology (33 pp.); neurobiology (25 pp.); life history (35 pp.); ecology (43 pp.); behavior (45 pp.); phylogeny, biogeography and taxonomy, including identification keys (44 pp.); field and laboratory techniques (13 pp.). The apparent absence of a logical structure both among and within the chapters inevitably leads to repetition, e.g., discussions of life history in the introduction (p. 8) and of behavior in the chapter on life history (p. 72). Some sections of Chapters 2, 3 and Chapters 4 and 6 would have benefited from a merger.

Valuable, if somewhat disproportionate coverage is devoted to the sections on natural history, habitat preference, diet composition, dispersion patterns, mating and hunting behavior, burrowing biology and diel/seasonal activity patterns (Chapters 4–6), many of which draw on data from the author's own studies. The final chapter provides important information on collecting and rearing solifuges, again drawn from the author's experience. Solifuges are notoriously difficult to maintain alive, let alone rear under captive conditions and the author is the only person on record to have successfully reared a species of solifuge through an entire generation (Punzo 1998).

Unfortunately, the sections presenting material outside of the author's expertise—anatomy, physiology and neurobiology (Chapters 2, 3) and phylogeny, taxonomy and biogeography (Chapter 7)—provide an unfavorable contrast with the sections on ecological and life history aspects, both in breadth of coverage and in accuracy of content. As previously noted by Hormiga (2000), the anatomical chapters are conspicuous for the paucity and poor quality of illustrations, including the complete absence of photographs (only 15 photographs appear in the entire book, all in Chapters 5, 6), while the chapter on systematics contains several inconsistencies. Most notable is the presentation of Van der Hammen's (1989) non-cladistic classification of the Chelicerata in Table 7-1 (p. 200), rather than the better justified system of Shultz (1990)—derived from a cladistic analysis of morphological data and recently supported by molecular data (Wheeler & Hayashi 1998)—which receives only secondary mention in the text (p. 202). The incomplete treatment of the chelicerate fossil record, with its implications for phylogeny have similarly been noted by Hormiga (2000). According to Fig. 7-1 (p. 198), Araneae are dated from the Carboniferous, despite Devonian spider fossils (Selden et al. 1991), while Solifugae are dated from the Tertiary, although the morphology of a Carboniferous solifuge is discussed a few pages later (pp. 211–214). To these errors and omissions can be added the inconsistent use of terminology, e.g., the old ordinal names Araneida, Scorpionida and Solpugida. On the positive side, this chapter provides a useful synthesis of identification keys, adapted from multiple sources, for the solifuge families of the world, as well as regional keys to the families and genera of North America (including Mexico), Israel and South Africa, and to the South American genera of Ammotrechidae. The book concludes with an extensive reference list (34 pp.)—more than 500 entries on all aspects of solifuge biology (33 by the author, though admittedly only 16 of these deal with solifuges)—itself a valuable introduction to the literature on the order. Indeed, the synthesis of such disparate information on solifuges from a large variety of scattered sources is certainly the most laudable aspect of a vol-

ume that will remain a landmark in the arachnological literature, despite its many shortcomings.

Whip Spiders, the second volume under consideration in this review, follows the tradition of Weygoldt (1969) in presenting another immaculately illustrated compendium on a remarkable order of arachnids. Both thorough content and impeccable presentation make for an unfair comparison with *The Biology of Camel-Spiders*. The publishers are similarly commended for the professional production of this volume.

The book is organized into nine chapters, dealing with the following topics: introduction to the Amblypygi (1 p.); historical background to studies on Amblypygi (2 pp.); external morphology (8 pp.); genera of Amblypygi, including identification key (16 pp.); anatomy and general biology, including behavior (87 pp.); distribution and ecology (9 pp.); endangered species (1 p.); systematics (7 pp.); field and laboratory techniques (2 pp.). These chapters are followed by a bibliography of selected references (7 pp.), no fewer than 33 by the author, but the reader is referred to a more extensive bibliography on the website of the International Society of Arachnology.

As with any such volume, there will always be differences of opinion as to how the subject matter could have been organized. For example, perhaps the large chapter on anatomy and general biology (Chapter 5) could have been split into smaller chapters and some of the smaller, but related chapters (e.g., Chapters 1, 2, Chapters 4 and 8, Chapters 6, 7) merged into larger, more inclusive units. Similarly, some subsections of particular chapters (e.g., the three lines on fighting and territoriality, p. 70) are arguably too short to warrant separate treatment and might have been better combined with others. But these are only minor criticisms of an excellent book overall.

As with his previous book on pseudoscorpions, the author demonstrates proficiency in all aspects of the biology of his subjects—from morphology, through ecology and distribution, to systematics—thereby rendering futile an attempt to find fault with the content. Aside from a distinct absence of errors and an unbiased treatment of conflicting opinions (e.g., the alternative hypotheses of chelicerate phylogeny presented in Chapter 8), the most obvious drawcard of this volume (subject matter notwithstanding) are the many exceptional illustrations that accompany each discussion as supporting evidence. Just as the sections on external morphology and anatomy are liberally illustrated with aesthetically appealing line drawings and clear electron micrographs, so the sections on behavior are illustrated with neat photographic sequences documenting ritualistic postures assumed in encounters between members of the same or opposite sex. Similarly, the sections on distribution, ecology and systematics are supported by maps, habitat photographs and cladograms, respectively.

The author is further commended for presenting the subject matter in a manner that is accessible and informative to both general and specialist readers alike. For example, by drawing on his extensive experience in the comparative morphology and systematics of Chelicerata, the author presents a detailed scientific synthesis and commentary of the characters relevant for delimitation and diagnosis of Amblypygi, as well as the phylogenetic relationships among them and their chelicerate relatives (Chapters 3, 4 & 8). However, the chapter on amblypygid genera should also be very useful to the general reader, for it includes not only a synopsis of each genus, accompanied by photographs of exemplar species, but a straightforward identification key. The sections on anatomy, behavior, distribution and ecology are equally comprehensive and bear testament to the author's many published scientific contributions. But the hard science is rendered accessible to the general reader by the regular inclusion of topics with broader interest, e.g., why are there so few species of Amblypygi, why is the courtship dance so prolonged and why do amblypygid females mate more than once.

Of all the topics covered, it is without doubt the author's meticulous studies on the complex mating behavior and related aspects of the reproductive biology of whip spiders (summarized in Chapter 5) that are most inspiring. During the past 30 years, the author has personally collected, transported and reared more than 20 species of Amblypygi for these studies, some of which are still maintained in laboratory colonies to this day. The difficulty in collecting many of these elusive animals in the wild, not to mention the patience required to maintain them and observe their nocturnal activities, whether in the field

or laboratory, demonstrate an uncommon dedication. *Whip Spiders* is yet another example of that dedication, and will certainly remain the standard text on Amblypygi for years to come, just as Weygoldt (1969) has remained the standard text on pseudoscorpions. I highly recommend this book as an essential addition to the libraries of all arachnologists.

LITERATURE CITED

Brownell, P.H. & G.A. Polis. (eds.) 2000. Scorpion Biology and Research. Oxford University Press, New York.

Fet, V., W.D. Sissom, G. Lowe & M.E. Braunwalder. 2000. Catalog of the Scorpions of the World (1758–1998). New York Entomological Society, New York.

Fet, V.A. & P.A. Selden. (eds.) 2001. Scorpions 2001: *In Memoriam* Gary A. Polis. British Arachnological Society, Burnham Beeches, Buckinghamshire.

Grassé, P. (ed.) 1949. Traité de Zoologie. Tome VI. Masson et Cie, Paris.

Harrison, F.W. & R.F. Foelix. (eds.) 1999. Microscopic Anatomy of Invertebrates: Chelicerate Arthropoda, Volume 8, Parts A–C. Wiley & Sons, Inc., New York.

Harvey, M.S. 1990. Catalog of the Pseudoscorpionida. Manchester University Press, Manchester.

Hormiga, G. 2000. Reviews: The Biology of Camel-Spiders (Arachnida, Solifugae). Systematic Biology 49:613–614.

Polis, G.A. (ed.) 1990. The Biology of Scorpions. Stanford University Press, Stanford, California.

Punzo, F. 1998. Natural history and life cycle of the solifuge *Eremobates marathoni* Muma, Brookhart (Solifugae, Eremobatidae). Bulletin of the British Arachnological Society 11:111–118.

Selden, P., W.A. Shear & P.M. Bonamo. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. Paleontology 34:241–281.

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6:1–38.

Van der Hammen, L. 1989. An Introduction To Comparative Arachnology. SPB Academic Publishing, The Hague.

Weygoldt, P. 1969. The Biology of Pseudoscorpions. Harvard University Press, Cambridge, Massachusetts.

Wheeler, W.C. & C.Y. Hayashi. 1998. The phylogeny of extant chelicerate orders. Cladistics 14:173–192.

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Lombardi, S.J. & D.L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (dragline) of *Nephila clavipes* (Araneae, Tetragnathidae). Journal of Arachnology 18:297-306.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15-66, *In* Spider Communications: Mechanisms and Ecological Significance.

(P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

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